The Effects of Mountain Landscapes on the Biodiversity Formation of Epigeic and Subterranean Arthropods: Community-wide Approach

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Takahiro OGAI

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Abstract

This thesis examines the effects of three potentially important but scarcely studied environmental axes of mountain landscapes: mountain topography, vegetation types, and landslides, on the biodiversity formation of epigean and subterranean arthropods using the community-wide approach. In Chapter 1, high- [*Carabus (Leptocarabus) arboreus*] and low-altitude [*C. (L.) procerulus*] carabid species were collected from 21 localities in and around the Japanese Alps and the sequences of two nuclear genes (total 1247 bp) from 37 and 36 individuals, respectively, were obtained. The results indicated that the within-species genetic differentiation of high-altitude species was higher than in low-altitude species. The landscape genetic analyses showed that low-altitude regions between mountains promoted genetic differentiation, particularly in high-altitude species, suggesting that mountain topography, consisting of ridges and valleys, promotes genetic differentiation in carabids. In Chapter 2, the community composition of epigeic Carabidae was studied by setting a total of 260 pitfall traps in 4–6 sites each of grassland, evergreen coniferous natural forest, deciduous broad-leaved natural forest, and deciduous coniferous plantation in the Sugadaira highlands, central Japan. The results indicated that vegetation types affected the community composition of carabid beetles. The species composition was the most different between grasslands and forests, and deciduous coniferous plantations had a large degree of overlap with the other two forest types. Thus, the effect of afforestation on carabid communities might be insignificant compared with the effects of cover types (deciduous vs. evergreen) and environmental factors. Each vegetation type hosted indicator species, suggesting that the four vegetation types maintain biodiversity at a regional landscape scale. In Chapter 3, the species-, family-, and order-level diversities of epigeic arthropods were studied in the same four vegetation types. The results showed higher arthropod diversity at larger temporal- and spatial-scales, and a tendency for higher spatial and seasonal heterogeneity in grasslands and deciduous broad-leaved forests compared to the two coniferous forests, suggesting that coniferous monoculture may limit arthropod diversity. In Chapter 4, the effect of landslides on the diversity and community composition of epigeic and subterranean arthropods was studied using baited traps in and around the Japanese Alps. The landside areas had higher arthropod abundances and order-level richness compared to undisturbed areas. More than one third of orders and families and half of species depended on landslide areas. The community composition in landslide areas was more endemic than in undisturbed areas. Thus, the environmental axis of landslides contributes greatly to local arthropod diversity. Overall, the results of all four chapters show that a mixture of environmental elements in an environmental axis contribute to arthropod genetic and taxonomic diversity. In Chapters 2–4, new species-, family-, and order-level bioindicators of scarcely studied environmental axes and environmental elements were found, which will help promote efficient environmental evaluation. Some families and orders of

arthropods did not depend on a particular environmental element along the axes of vegetation type and landslides, while all species were indicators of a particular environmental axis, suggesting species-level habitat specialization. Grasslands and landslides were also found to harbor large numbers of bioindicators, suggesting that landscapes including these spatially limited environmental elements increase regional arthropod diversity. While grasslands contribute to species-level diversity, landslides contribute to order- and family-level diversity, suggesting that different environmental axes can affect arthropod diversity and community composition at different taxonomic levels.

General Introduction

Japan is one of the world's biodiversity hotspots (Jenkins et al. 2013). High biodiversity in Japan is thought to be driven by the diversity of geological and topological features formed by the tectonic activities of the four crustal plates interacting on and around the country. A diversity of geological features is particularly notable in mountainous regions, where high biodiversity is also observed. For example in South America, the uplift of the Andes mountains changed the Amazonian landscape and caused the development of a region-wide mosaic of environments that is extremely rich in species (Hoorn et al. 2010). In the Japanese mountains, especially in and around Japanese Alps, there is a complex topography with eight discontinuous mountain ranges and lowland areas. Biodiversity in relation to these features, there are four climatic zones (i.e. boreal, sub-boreal, cool-temperate, and temperate zone) and high animal and plant diversity maintained by the multiple climatic zones. The abundant biodiversity (species diversity and interactions among species) has an important role to stabilize ecosystem (Yamamura 2002; Mougi and Kondoh 2012). The monitoring of the biodiversity is necessary not only conservation of rare species but also understanding stability of the whole ecosystem.

The study of biodiversity by investigating a relatively wide range of taxonomic groups is known as the community-wide approach (Martin and Eadie 1999;Pugnaire et al. 2004). This approach enables a comprehensive understanding of the distributions and changes in diversity. The diversity of wide-range of taxonomic groups can be a good environmental indicator because different taxonomic groups react differently to environmental changes (Kotze and Samways 1999a, 1999b; Oertli et al. 2005). For example, taxonomic diversity is more sensitive to anthropogenic disturbance than species richness (Warwick and Clarke 1998; Campbell and Novelo-Gutiérrez 2007; Moreno et al. 2009). One drawback of the community-wide approach is that enormous sampling and identification efforts are required. To reduce these efforts, bioindicators, a subset of taxa known to be sensitive to environmental changes are often used. For example, birds, butterflies, and beetles (Carabidae and Staphylinidae of Coleoptera) have been used as bioindicators to monitor the effect of natural vegetational succession (Bohac 1999; Inoue 2003; Herkert 2012) and urbanization (Chace and Walsh 2006; Johns 2009). An additional important consideration is the spatial scale at which biodiversity assessments are performed.

Biodiversity can be assessed across a range of scales such as genetic diversity, species diversity, and landscape diversity. A 'landscape' can be defined as the composition of multiple environmental elements in one or more environmental axes and such landscapes have been studied in relation to macro-scale biodiversity (Office of Technology Assessment 1987). Mountains have many environmental axes (e.g. elevation, disturbance, soil conditions) with each consisting of various environmental elements (e.g. low–high altitude, disturbed / undisturbed, low–high pH) that are known to influence biodiversity. For example, elevation affects species distribution patterns and

species richness (Becker et al. 2007); natural disturbances, such as fire and avalanche, create environmental heterogeneity and intermediate disturbance increases species diversity of plants (Bebi et al. 2009; Perry et al. 2011); intensive artificial disturbances, such as agriculture and plantations, are negatively correlated with biodiversity (Kocher and Williams 2000; Schmitzberger et al. 2005; Agnoletti 2007); soil pH and calcium content positively affect species richness of vascular plants in central Europe (Chytrý et al. 2003); and changes in aerial moisture are highly correlated with species composition of birds in Costa Rica (Jankowski et al. 2009). However, there are several other landscape features that may be influencing biodiversity but are yet to investigated.

In this thesis, I studied the role of several, previously seldom explored, features of mountain landscapes on biodiversity formation, focusing on three environmental axes: mountain topography, vegetation types and landslides. In particular, I explored the potential effects of a combination of these different environmental elements on epigeic and subterranean (above- and below-ground respectively) invertebrate biodiversity using bioindicator taxa. Invertebrates comprise the bulk of animal species diversity and they are distributed over broad habitat and geographical ranges. For example one invertebrate class, Arthropoda (arthropods), has the highest species richness amongst all classes (Wilson 1988; Zhang 2011), and can be regarded as a key contributor to biodiversity. Litter-dwelling arthropods such as Acari, Collenbola, and Myriapoda, and soil-dwelling arthropods such as some groups of Hexapoda, have low dispersal abilities and are easily affected by environmental changes, thus they are suitable indicators to evaluate the effect of environmental change.

The environmental axis addressed in Chapter 1 was mountain topography, which forms at geological time-scales, meaning that a more long-term reflection of biodiversity, such as an evolutionary approach, is appropriate. Thus to study the effect of mountain topography on genetic differentiation, I focused on one taxonomic group, the subgenus *Leptocarabus* (Coleoptera: Carabidae). The environmental axis addressed in Chapters 2 and 3 is vegetation type. Vegetation type is an environmental axis that changes over a time-scale of several hundred years, for example by successions and afforestation. At this time-scale, biological communities are formed through migration, establishment, and local extinction. To study such community formation and diversity in arthropods, I targeted two relatively large taxonomic groups, the Carabidae family in Chapter 2 and the Arthropoda class in Chapter 3. The final environmental axis, addressed in Chapter 4, was landslides, including shallow landslides that occur rather consistently, and deep-seated landslides that occur suddenly. Disturbed habitats generated by landslides remain for several tens to hundreds of years, a time-scale at which, once again, species migration, establishment and local extinction determine community formation. To explore the effects of landslides on biodiversity and community composition, I studied both epigeic and subterranean arthropods, as a rich suite of endemic fauna has recently been found living under landslides (Culver and Pipan 2008; Ito 2010; Barranco et al. 2013; Sugaya and Yamasako 2014; Olmi et al. 2014).

Through these four chapters, I aimed to: i) test the role of mountain landscapes in shaping genetic and community diversity; ii) search for new bioindicators for particular environmental axes and elements; and iii) examine whether the taxonomic levels of bioindicators differ between environmental axes, exploiting the community-wide approach.

Chapter 1:
Genetic differentiation within two *Leptocarabus* carabid beetle species that inhabit different altitudinal zones.

Although this study suggested an effect of mountain topography, or low-altitude zones between mountain regions, in promoting genetic differentiation of high-altitude species, there are other possible geographic barriers, not investigated here that may also have an effect. In this study, first-class rivers had no effect on genetic distance (Table 1-3), possibly because the distribution and branching of rivers has been variable over time. In addition, both species are distributed over 2000m a.s.l. (Sota 1996; Hiramatsu 2002), where the width of rivers are narrower, therefore might not be a significant geographic barrier to both *Leptocarabus* beetles studied here.

Tables of Chapter 1

Table 1-1 The number of samples collected and used for DNA analyses of *Carabus (Leptocarabus) arboreus*.

Subspecies	Mountain Region	Site	N	E	Number of collected individuals	Number of individuals used for DNA analyses
Carabus (Leptocarabus) arboreus gracillinus	The Central Japanese Alps	Mt. Eboshigatake	35.65246	137.84606	3	2
	The Central Japanese Alps	Mt. Kisokomagatake	35.81004	137.82591	7	2
	The Northern Japanese Alps	Mt. Norikura	36.1191	137.59379	5	2
	The Northern Japanese Alps	Mt. Nishihotaka	36.26773	137.61664	8	2
	The Northern Japanese Alps	Mt. Jigatake	36.5878	137.73526	8	2
C. (L.) arboreus horioi	The Southern Japanese Alps	Ikawa Forest of the University of Tsukuba	35.35458	138.21484	2	2
	The Southern Japanese Alps	Mt. Senjogatake	35.72958	138.19841	15	2
	The Southern Japanese Alps	Mt. Myugasayama	35.89753	138.17292	1	1
C. (L.) arboreus ogurai	Mt. Chichibu	Mt. Kokushigatake	35.88725	138.66349	54	2
	Mt. Chichibu	Mt. Mitsutogeyama	35.55049	138.81042	28	2
	Mt. Chichibu	Mt. Nanatsuishiyama	35.82974	138.96172	6	2
C. (L.) arboreus fujisanus	Mt. Fuji	Fifth station of Mt. Fuji	35.38617	138.75923	5	2
C. (L.) arboreus tenuiformis	Joshin'etsu highland	Mt. Kasagatake	36.67682	138.48121	13	2
	Joshin'etsu highland	Mt. Koasamayama	36.42235	138.57079	1	1
	Joshin'etsu highland	Mt. Yunomaruyama	36.41691	138.44414	2	2
C. (L.) arboreus babai	Mt. Myoko	Mt. Gojizosan	36.79066	138.06923	13	2

	Mt. Myoko	Mt. Myokosan	36.89261	138.12439	23	2
C. (L.) arboreus	Mt. Yatsugatake	Mt. Yokodake	35.98348	138.37683	5	2
shinanensis	Mt. Yatsugatake	Mt. Gongentake	35.94053	138.36574	5	2
	Mt. Yatsugatake	Mt. Takeshimine	36.25991	138.0969	1	1
Total					205	37

Table 1-2 The number of samples collected and used for DNA analyses of *Carabus (Leptocarabus) procerulus*.

Subspecies	Mountain Region	Site	N	E	Number of collected individuals	Number of individuals used for DNA analyses
Carabus (Leptocarabus) procerulus	The Central Japanese Alps	Mt. Eboshigatake	35.65246	137.84606	8	2
	The Central Japanese Alps	Mt. Kisokomagatake	35.81004	137.82591	8	2
	The Northern Japanese Alps	Mt. Norikura	36.1191	137.59379	6	2
	The Northern Japanese Alps	Mt. Nishihotaka	36.26773	137.61664	71	2
	The Northern Japanese Alps	Mt. Jigatake	36.5878	137.73526	96	2
	The Southern Japanese Alps	Mt. Nyugasayama	35.89753	138.17292	4	1
	The Southern Japanese Alps	Ikawa Forest of the University of Tsukuba	35.35458	138.21484	4	2
	Mt. Chichibu	Mt. Mitsutogeyama	35.55049	138.81042	3	2
	Mt. Chichibu	Mt. Nanatsuishiyama	35.82974	138.96172	2	2
	Mt. Fuji	Mt. Oyama	35.44122	139.23083	1	1
	Joshin’etsu highland	Mt. Kasagatake	36.67682	138.48121	3	2
	Joshin’etsu highland	Mt. Kurohimeyama	37.22406	138.599	8	2
	Joshin’etsu highland	Mt. Azumayasan	36.53673	138.38785	3	2
	Joshin’etsu highland	Mt. Hishigatake	37.0271	138.49173	1	1
	Joshin’etsu highland	Mt. Koasamayama	36.4056	138.56664	5	2
	Mt. Myoko	Mt. Gojizosan	36.79066	138.06923	10	2
	Mt. Myoko	Mt. Myokosan	36.89261	138.12439	5	1
	Mt. Yatsugatake	Mt. Gongentake	35.94053	138.36574	1	1

	Mt. Yatsugatake	Fukinotaira	36.13219	138.28054	1	1
	Mt. Yatsugatake	Mt. Takeshimine	36.25991	138.0969	20	2
	Mt. Yatsugatake	Mt. Washigamine	36.14435	138.14595	13	2
Total					273	36

Table 1-3 The effects of three geographic barriers, represented by different resistances, on genetic distance (total number of nucleotide substitutions in two nuclear genes: 28s rDNA and *Wingless*, total=1247 bp) in two *Leptocarabus* species by permutational regression analysis. *The regression coefficients and the levels of significance are shown* (*** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 1000 permutations).

Species	Resistances		
	Horizontal	Low-altitude	River
Carabus (Leptocarabus) arboreus	0.359	3.906 *	1.959
Carabus (Leptocarabus) procerulus	1.338	0.676	0.203

Figures of Chapter 1

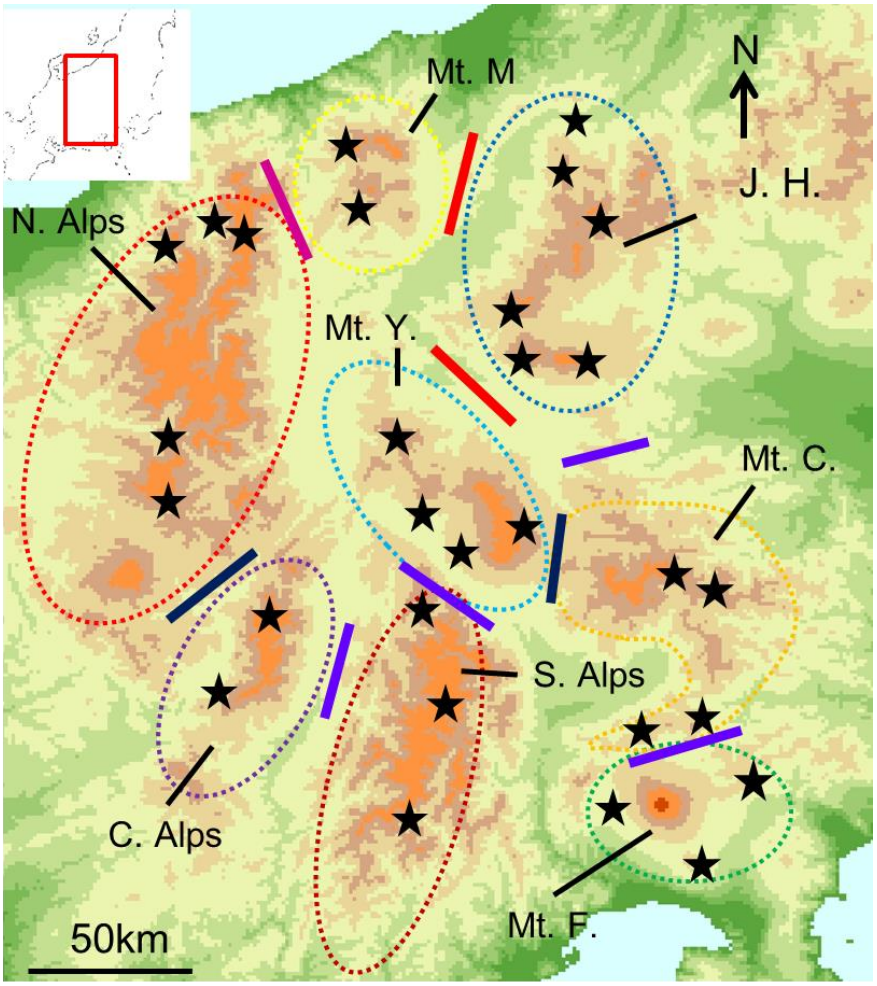

Fig. 1-1 Map showing the study region. Black stars indicate sampling locations. The colors of border lines of mountain regions correspond to those in Fig 1-2. The bars between mountain regions indicate altitude saddles: blue = greater than 1000 m a.s.l.; purple = 751–1000 m a.s.l.; pink = 501–750 m a.s.l.; and red = 250–500 m a.s.l.. Region names are abbreviated as follows: N. Alps = the Northern Japanese Alps; C. Alps = the Central Japanese Alps; S. Alps = the Southern Japanese Alps; Mt. M = Mt. Myoko; J. H. = Joshin'etsu highland; Mt. Y. = Mt. Yatsugatake; Mt. C. = Mt. Chichibu; and Mt. F = Mt. Fuji.

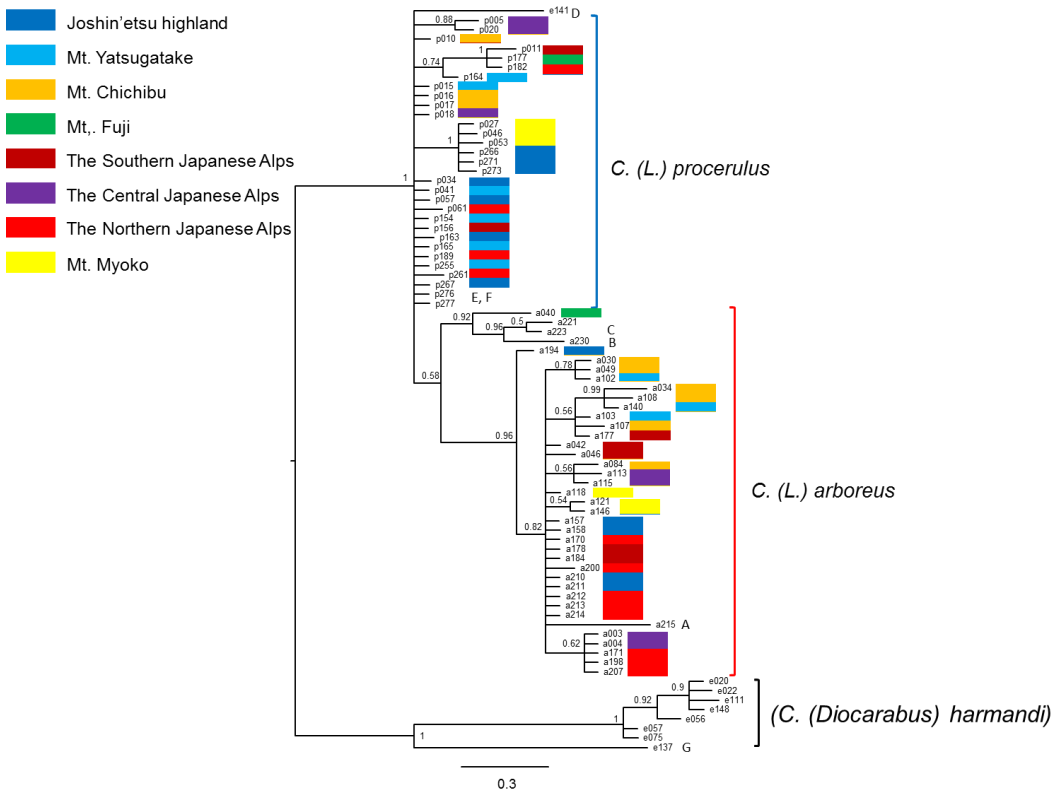

Fig. 1-2 Combined nuclear 28s and *Wingless* gene (1247 bp) tree (50% majority consensus phylogram resulting from Bayesian analysis). The numbers at the end of branches show the individual sample names, and colored squares indicate where the samples were collected. The reference samples and out-groups are indicated by capital letters: A = *C. (L.) arboreus gracillinus* (Aizuwakamatsu city, Fukusima Pref.); B = *C. (L.) arboreus ishikarinus* (Chitose city, Hokkaido Pref.); C = *C. (L.) arboreus nepta* (Rokkasho village, Aomori Pref.); D = *C. (L.) hiurai* (Kamegamori, Ehime Pref.); E and F = *C. (L.) procerulus* (Miyako city, Iwate Pref.); and G = *C. (D.) opaculus* (Urahoro city, Hokkaido Pref.). Numerals on branches are posterior probabilities (proportions) resulting from Bayesian analysis.

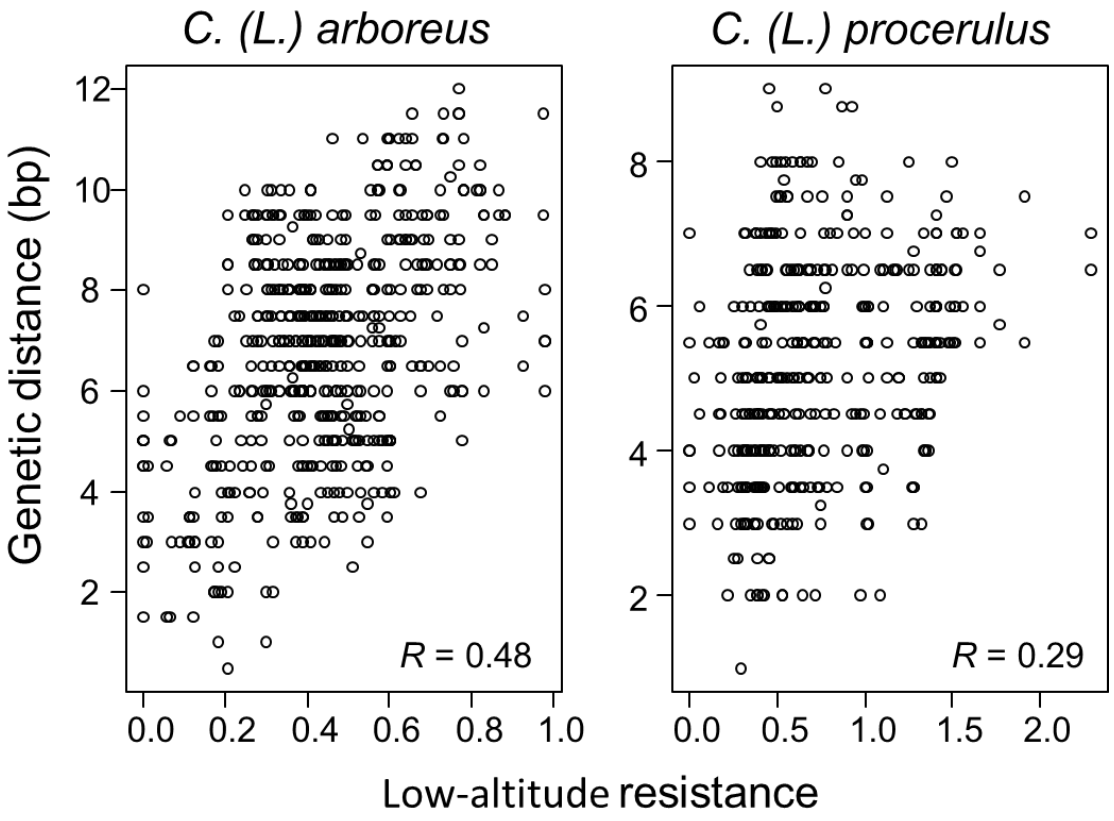

Fig. 1-3 The scatter plots of genetic distance (total number of nucleotide substitutions in two nuclear genes: 28s rDNA and *Wingless* total=1247 bp), and low-altitude resistance in two *Leptocarabus* species. Pearson's product moment correlation coefficients are shown.

Chapter 2:
The effects of vegetation types and microhabitats on carabid beetle community composition.

2-1 Introduction

Spatial and temporal heterogeneity in vegetation caused by natural succession (e.g. from grassland to forest) and human activities (e.g. deforestation and afforestation) has a strong impact on biodiversity, including insect communities (Fahy and Gormally 1998; Magura et al. 2001; Magura et al. 2003; Driscoll and Weir 2005; Fuller et al. 2008; Niemelä and Kotze 2009). However, because of the time and cost required by large-scale comprehensive biodiversity surveys, indicator species have often been used as a practical yet accurate estimator of the impacts of environmental changes on biodiversity. In studies of the effects of spatial and temporal environmental variation on insect biodiversity, carabid beetles (Coleoptera: Carabidae) are regarded as suitable bioindicators because of the variation in their life-history traits (e.g. good dispersers vs. bad dispersers, carnivores vs. herbivores, specialists vs. generalists) and their sensitivity to changes in vegetation type and microhabitat conditions (Rainio and Niemela 2003; Baker 2006; Maleque et al. 2009; Hopp et al. 2010; Fountain-Jones et al. 2015).

Previous studies of carabid beetle community composition have detected significant differences across vegetation types (Butterfield et al. 1995; Heliola et al. 2001; Magura et al. 2001; Kattan et al. 2006; Karen et al. 2008). For example, grasslands host large numbers of winged and smaller-sized species (Driscoll and Weir 2005; Niemelä and Kotze 2009; Shibuya et al. 2014), indicating that grasslands might play an important role in maintaining or increasing biodiversity at a regional landscape scale. In addition, many studies in Europe have stressed the differences in carabid species composition between evergreen coniferous plantations and deciduous broad-leaved natural forests (Fahy and Gormally 1998; Magura et al. 2003; Fuller et al. 2008). However, these studies have not separated the effect of cover type (i.e. deciduous vs. evergreen and broad-leaved vs. coniferous) from that of afforestation (i.e. natural forest vs. plantation). Indeed to differentiate between all of these factors, especially within a given climatic zone, is difficult. To date, only three studies in China have examined combinations of cover type and afforestation, e.g. deciduous coniferous plantation (Yu et al. 2006; Yu et al. 2008; Warren-Thomas et al. 2014) and evergreen coniferous natural forest (Yu et al. 2008); it was found that the number of significant indicator species was higher in deciduous broad-leaved natural forest than in deciduous coniferous plantation (Yu et al. 2006; Yu et al. 2008) and evergreen coniferous natural forest (Yu et al. 2008). Although these studies showed that carabid community composition tended to differ between natural and artificial forests, the effects of afforestation were also influenced by forest age and study site. Given that the majority of studies have been performed in Europe (i.e. evergreen coniferous plantations and deciduous broad-leaved natural forests), the exploration of different forest types and combinations of cover types and afforestation is warranted to better understand carabid community composition and habitat preferences for different vegetation types.

The study of microhabitat characteristics is important in understanding carabid community

composition and habitat preference and might lead to a mechanistic explanation of the relationship between community composition and vegetation type. For example, some species might prefer a certain vegetation type because of specific environmental factors that are closely associated with that vegetation type. Some environmental factors are known to influence the abundance and species richness of carabid beetles, including canopy gaps (Antvogel and Bonn 2001; Pinna et al. 2008), understory vegetation (Antvogel and Bonn 2001; Magura et al. 2001; Magura 2002; Tyler 2008), litter depth or soil O-horizon (Guillemain et al. 1997; Magura et al. 2000; Antvogel and Bonn 2001; Magura 2002; Magura et al. 2005), and soil hardness (Cole et al. 2002; Magura 2002; Magura et al. 2003). Recently, because of advances in statistical analyses for community ecology, canopy openness (Antvogel and Bonn 2001; Barton et al. 2009), soil moisture and soil pH (Antvogel and Bonn 2001), as well as cover of litter (Antvogel and Bonn 2001; Fountain-Jones et al. 2015) and herbs (Antvogel and Bonn 2001) have been shown to affect carabid community composition. However, there might be other important unexplored factors affecting carabid communities. For example, whilst depth of the soil A-horizon and cover of dwarf bamboo (Ueda et al. 2009) have been shown to affect other ground animal communities and some species of carabids (Nojima et al. 2013, Ueda et al. 2009), their effects on carabid community composition have been scarcely studied.

In this study, I examined carabid community composition in response to varying vegetation types and seven micro-environmental factors, and characterized those communities in each vegetation type by indicator species analyses. The studied vegetation types were representative of cool temperate Japan and consisted of grassland, evergreen coniferous natural forest, deciduous broad-leaved natural forest, and deciduous coniferous plantation. These vegetation types, particularly deciduous coniferous plantations and evergreen coniferous natural forests, provided combinations of cover type and afforestation that have been poorly studied in relation to carabid communities. The specific aims of the study were to: i) validate the uniqueness of the grassland carabid community in an Asian cool temperate region, a seldom-studied system; ii) examine the effect of afforestation compared with cover type and environmental factors; and iii) test the prediction that depth of the soil A-horizon and cover of dwarf bamboo, which have been scarcely studied in relation to carabid communities, have important effects on carabid community composition.

2-2 Materials and methods

Study sites and sample collection

Study sites were located in and around Sugadaira Montane Research Center, University of Tsukuba (36°31’N, 138°20’E, 1240–1490 m a.s.l.) in central Japan. The climate of the region is cool temperate, with mean annual temperature of 6.8 °C; the mean temperature of the warmest month in

Figures of Chapter 2

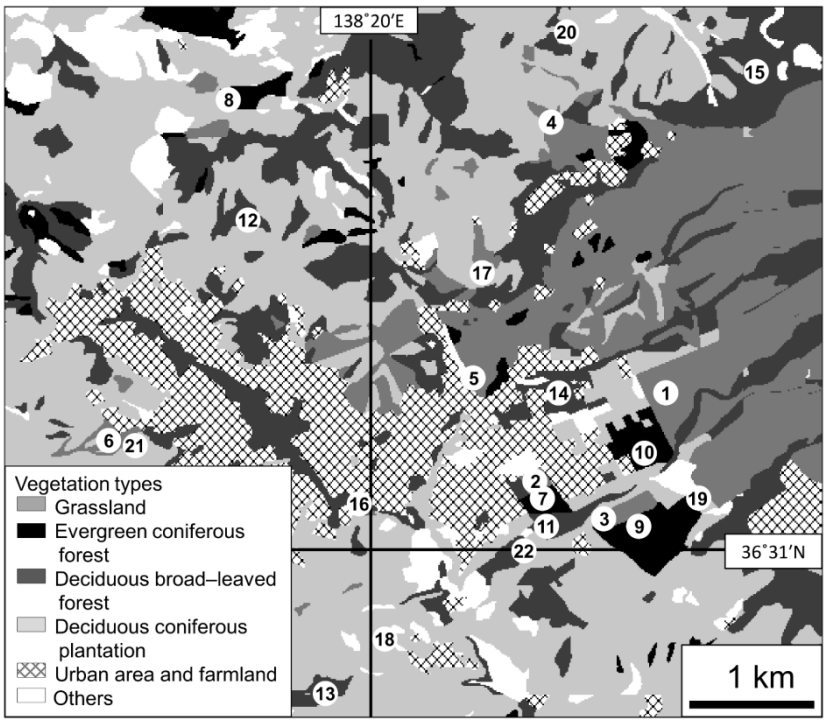

Fig. 2-1 The landscape of the study area [Modified from GIS data of 1:25,000 scale vegetation map (Biodiversity Center of Japan) and Tanouchi and Hayashi (1981)]. The numbers of the study sites correspond to those in Table 1.

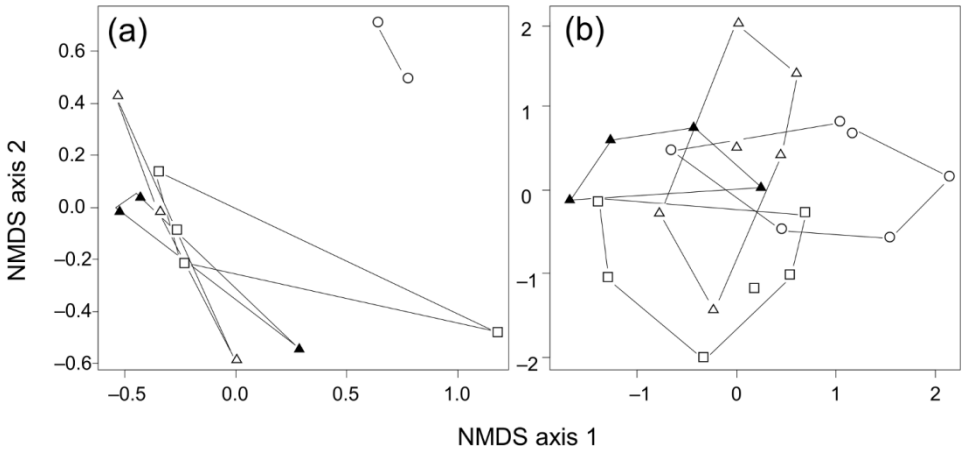

Fig. 2-2 Ordination plot non-metric multidimensional scaling (NMDS) using Horn–Morisita index of dissimilarity of the range of community composition of grassland (open circle), evergreen coniferous *Pinus* forest (filled triangle), deciduous broad-leaved forest (open square), and deciduous coniferous *Larix* plantation (open triangle) in the (a) early, and (b) late surveys.

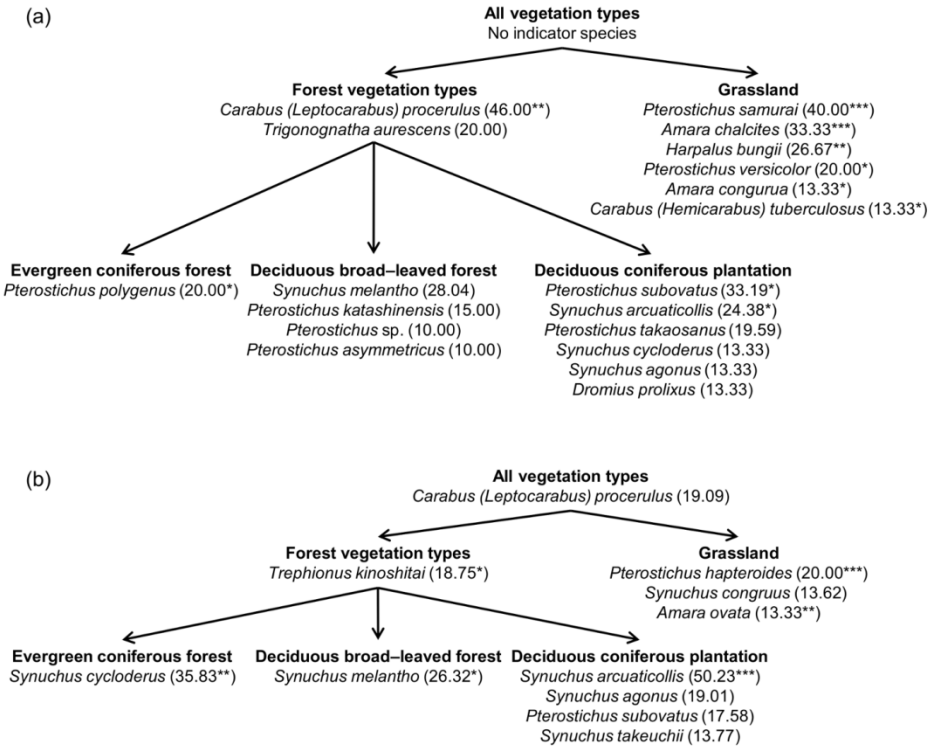

Fig. 2-3 Tree diagram of the vegetation types with the associated indicator species values (values greater than 10% in parentheses) for the (a) early, and (b) late surveys. The significance levels of the species indicator values were shown (*** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 9999 permutations).

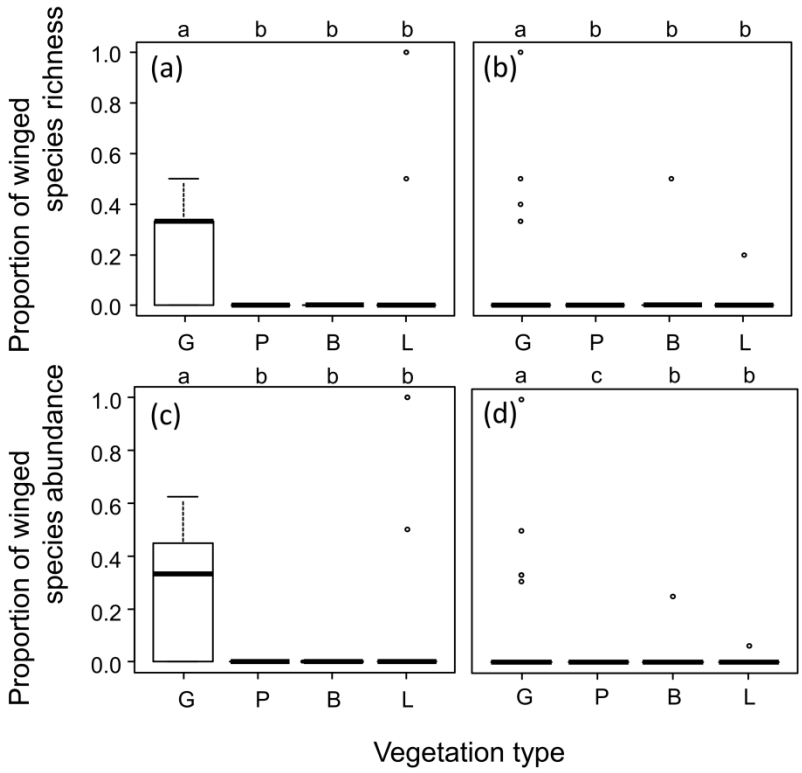

Fig. 2-4 Box plots of the proportion of winged species richness (a, b) and abundance (c, d) in each vegetation type for the early and late surveys, respectively. Vegetation types with different letters have significantly different means, according to the model selection using generalized linear models (GLMs). The boxes indicate the lower quartile, median, and upper quartile. The whisker lines extend from lower quartile − 1.5 × interquartile range (IQR) to upper quartile + 1.5 × IQR. Dots represent data points beyond the ends of the whiskers. G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation.

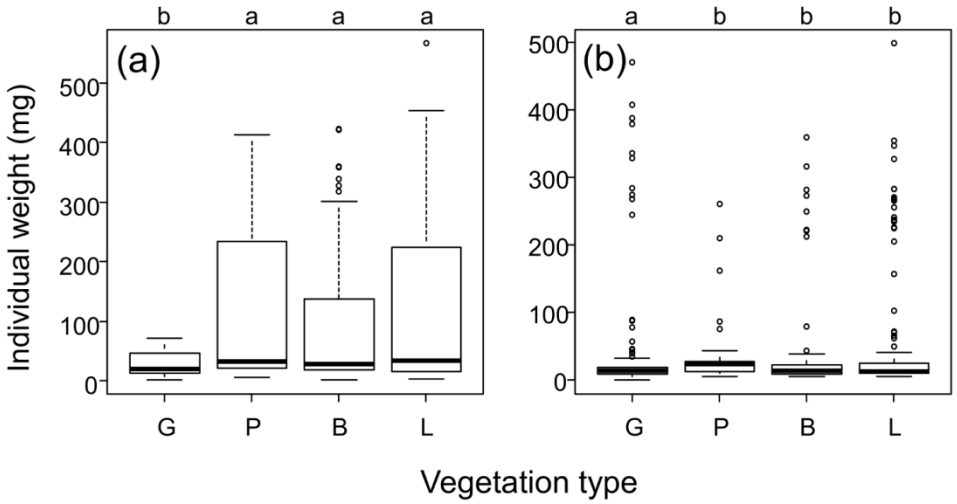

Fig. 2-5 Box plots of individual body weights in each vegetation type in the (a) early, and (b) late surveys. Vegetation types with different letters have significantly different means, according to the model selection using generalized linear models (GLMs). The boxes indicate the lower quartile, median, and upper quartile. The whisker lines extend from lower quartile − 1.5 × interquartile range (IQR) to upper quartile + 1.5 × IQR. Dots represent data points beyond the ends of the whiskers. G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation.

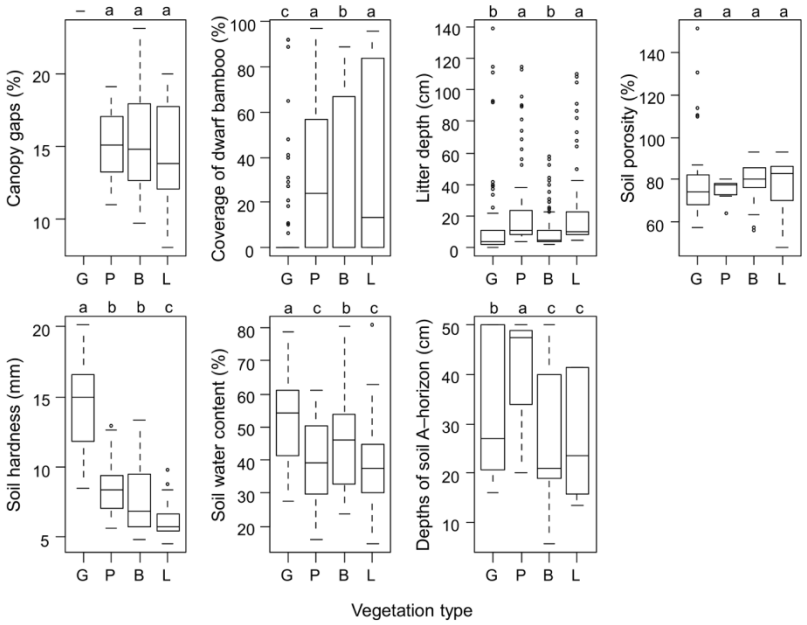

Figure 2-6. Box plots of seven environmental factors in each vegetation type. Vegetation types with different letters have significantly different means, according to the model selection using generalized linear models (GLMs). The boxes indicate the lower quartile, median, and upper quartile. The whisker lines extend from lower quartile − 1.5 × interquartile range (IQR) to upper quartile + 1.5 × IQR. Dots represent data points beyond the ends of the whiskers. G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation. We did not measure canopy gaps in the grassland.

Chapter 3:
Vegetation affects the diversity of ground-dwelling animals differently depending on the spatial- and temporal-scales and taxonomic-level.

3-1 Introduction

Vegetation type is a good indicator of human influence (Mckinney and Michael 2002; Ishitani et al. 2003; Chace and Walsh 2006) and is one of the important factors that determine the diversity of animals (Herkert 2012; Pryke and Samways 2011; Schuldt and Scherer-Lorenzen 2014) and as such can provide insights on how human activity affects animal diversity. The ground dwelling taxa of the Arthropoda phylum (arthropods), which have low dispersal abilities, may be particularly affected by environmental changes. Moreover, the Arthropoda has the highest number of species of all phyla (Wilson 1988; Zhang 2011), the number of individuals are abundant, and the body size is small, so they are easily collected and quantified. For these reasons, the arthropods have been used as indicator animals for environmental changes (e.g. afforestation and forest management). Previous studies on landscape ecology using arthropods have focused on particular orders, e.g. Acari, Collembola, Isopoda, and Araneae (Hassall et al. 2006; Ribeiro-Troian et al. 2009; Cakir and Makineci 2013; Schuldt and Scherer-Lorenzen 2014), or families, e.g. Formicidae, Carabidae, Cerambycidae, and Staphylinidae (Kotze and Samways 2001; Ohsawa 2004; Maleque et al. 2009; Vásquez-Vélez et al. 2010) and have evaluated their objectives using particular characters of each taxon. In contrast, studies including all arthropod groups are rare [but see Kattan et al. (2006); Pryke and Samways (2011)]. Taxonomic diversity, which takes the diversity of higher taxonomic levels into consideration, rather than just species richness, has huge potential as a complementary measure of environmental impact assessment (Warwick and Clarke 1998). Taxonomic diversity has been used to compare the diversity of vascular plants between native forests and secondary forests (Moreno et al. 2009), to detect the effect of disturbance on aquatic ecosystems (Salas et al. 2006; Marchant 2007), and to investigate dragonfly communities (Campbell and Novelo-Gutiérrez 2007). Therefore, investigating the diversity and distribution of all arthropods in the environment is very important for understanding a large component of local biodiversity.

There are many studies comparing the diversity of ground-dwelling arthropods among vegetation types to evaluate the effect of anthropogenic disturbances. For example, grasslands had higher species richness or diversity of the family Carabidae than forest vegetation types (evergreen coniferous plantations or deciduous broad-leaved natural forests: Butterfield et al. 1995; Heliola et al. 2001; Magura et al. 2001; Karen et al. 2008), but the diversity of the family Formicidae was higher in forests than grasslands (Kotze and Samways 2001). Thus, the biodiversity detected in grasslands and forests can depend on the taxonomic group studied. Despite this, there are no studies investigating wide taxonomic groups of arthropods and comparing grasslands and forests in the temperate zone of Asia. In addition, many studies have compared differences in arthropod diversity between evergreen coniferous

plantations and deciduous broad-leaved natural forests but have not separated the effect of cover types (i.e. deciduous vs. evergreen and broad-leaved vs. coniferous) from that of afforestation (i.e. natural forest vs. plantation). Those studies found that the diversities of the orders Acari, Collembola, and Araneae, and the families Carabidae and Cerambycidae were higher in deciduous broad-leaved natural forests (Maeto et al. 2002; Fuller et al. 2008; Cakir and Makineci 2013; Schuldt and Scherer-Lorenzen 2014).In addition, some studies of the Carabidae or Chrysomelidae showed that species richness was higher in deciduous coniferous plantations compared to deciduous broad-leaved natural forests (Ohsawa and Nagaike 2006; Yu et al. 2008), while the majority of other studies investigating the Carabidae, Curculionidae, and Staphylinidae families have suggested that species richness is higher in deciduous broad-leaved natural forests compared to deciduous coniferous plantations (Ohsawa 2005; Yu et al. 2006; Luo et al. 2013). Thus, it is clear that the examination of wider taxonomic groups is required to determine which types of vegetation host a more diverse array of arthropods.

The total diversity in a landscape (gamma) is determined by local or habitat scale diversity (alpha) and the differences in diversity among habitats (beta). Alpha diversity at a particular spatial scale is only a part of the total diversity (Whittaker 1977; Gering et al. 2003), and partitioning diversity into several spatial scales provides useful insights regarding the structure and heterogeneity of biological communities (Weiher and Howe 2003). For example, a region with high habitat heterogeneity could have a higher within-region beta diversity and higher broad-scale alpha diversity than another region that has a higher narrow-scale alpha diversity. Several studies have examined such spatial heterogeneity by calculating beta diversities (Davis et al. 2001; Magura et al. 2003; Clough et al. 2007), or by spatial accumulation curves in taxonomic richness, or rarefaction curves (Barton et al. 2010; Grimbacher et al. 2007; Fagundes et al. 2011). Microhabitat factors are also important in understanding arthropod abundance and diversity and may lead to a mechanistic explanation of the relationship between diversity and vegetation type. Some environmental factors, including canopy gaps (Yi and Moldenke 2005; Maleque et al. 2007; Yi and Moldenke 2008; Taki et al. 2010), understory vegetation (Ribeiro-Troian et al. 2009 ; Eisenhauer et al. 2011), and litter depth or soil O-horizon (Ober and DeGroote 2011, 2014), are known to influence the abundance and diversity of some orders and families of arthropods. However, there could be other important unexplored factors affecting arthropod diversity. For example, whilst depth of the soil A-horizon and cover of dwarf bamboo (Ueda et al. 2009) have been shown to affect some components of ground animal diversity, including some species of carabids (Nojima et al. 2013, Ueda et al. 2009), their effects on the total diversity of arthropods have been scarcely studied.

In addition to assessing diversity at these spatial scales, diversity can also be assessed at different temporal scales. Yet, temporal (seasonal) scale heterogeneity has been

scarcely examined. Usually researchers collect samples in various seasons, and may find variable activity and abundance of arthropod species (Rainio and Niemela 2003). Such seasonal heterogeneity can be an important element of biodiversity and may be particularly important in understanding regional biodiversity if different vegetation types have different levels of temporal heterogeneity.

In this chapter, the diversity of ground-dwelling arthropods in four vegetation types: grassland, evergreen coniferous natural forest, deciduous broad-leaved natural forest and deciduous coniferous plantation, was investigated. The effect of several environmental factors in these vegetation types was also examined, in order to understand the mechanisms by which vegetation types affect animal diversity. Sample data was collected by the same set of pitfall traps as utilized in Chapter 2, but was sorted and identified using wider taxonomic groups (orders of the kingdom Animalia, families of the order Coleoptera, and the species of the family Carabidae). The following questions were addressed: 1) which vegetation type harbors a high diversity of arthropods at (i) high taxonomic level, and ii) various spatial- and temporal-scales, and 2) does the depth of the soil A-horizon and cover of dwarf bamboo, which have been scarcely studied, affect arthropod and carabid diversities.

3-2 Methods

Study sites and sample collection

This chapter used samples collected by some of the traps used in Chapter 2. To equalize the number of sites and traps for each vegetation type for each season, site No. 13 was excluded from deciduous broad-leaved natural forests, and in the other sites data from traps set during both early and late surveys was used. The exclusion of site No. 13 also made sites of deciduous broad-leaved natural forest more uniform, as site No. 13 was dominated by *Fagus crenata* while the other sites were dominated by *Quercus crispula.* This sampling design resulted in a total of 3 sites, 15 plots, and 150 traps for each survey in four time periods: June, July, September, and October, and four vegetation types: grassland, evergreen coniferous natural forest, deciduous broad-leaved natural forest, and deciduous coniferous plantation. All animals larger than 1 mm, including larvae, were identified to order-level following Aoki (1999), and all adults of the order Coleoptera were identified to family-level following Kurosawa et al. (1985), Ueno et al. (1985) and Hayashi et al. (1984). The species identifications for the family Carabidae made in Chapter 2 were utilised here. The data of seven environmental factors measured in Chapter 2: canopy openness (hereafter, canopy gaps), soil hardness, soil porosity, soil water content, depth of the soil A-horizon, coverage of dwarf

bamboo, and litter depth at all surveys, were also used here.

Statistical analyses

To examine the effect of vegetation types on taxonomic diversities at (i) small- and (ii) large-spatial scales for each taxonomic level, generalized linear models (GLMs) were analysed in *R* ver. 2.10.1 (*R* Core Team 2012). The dependent variables were number of: orders (of all animals), families (of Coleoptera) or species (of Carabidae), summed for each plot for (i), and each vegetation type for (ii). Each dependent variable was fitted to a linear predictor:

$\mu \sim \beta_0 + \beta_1 V$,

where μ was each dependent variable, β_0 was an intercept, β_1 was an estimator of the coefficient of V, and V was the categorical variable for groups of vegetation types (described below). The link function of the linear predictor μ was log μ for analyses (i) and (ii). The error distribution of μ was Poisson. To examine the specific effects of each vegetation type, all 15 possible cases were reconstructed, with the four vegetation types being divided into one, two, three, or four group(s), i.e. (G, B, L, P), (G, B) (L, P), (G) (B) (L, P), and (G) (B) (L) (P), respectively (G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation). The model where the four vegetation types were treated as one group was designated as the null model. The fitness of all constructed models was evaluated based on Akaike's information criterion (AIC: Akaike (1973)) and the model with the lowest AIC was selected as the best.

The presence of each taxon per survey, calculated for every plot, was assessed by a sample-based accumulation curve (e.g. Hurlbert 1971; Heck et al. 1975; Novotny and Basset 2000) of each taxonomic level (i.e. order-level of the kingdom Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae) for every vegetation type (1,000 randomizations in *R*). Accumulation curves were then used to standardize sampling effort by randomly selecting from the sampling set (e.g. traps and plots). Four kinds of sample-based accumulation curves were calculated: spatial, temporal, spatial and temporal, and spatial and temporal accumulation curves of three mixed vegetation types. For the spatial accumulation curves, taxonomic richness per plot throughout the four surveys for each vegetation type was counted (total of 15 plots per vegetation type). Then, 15 plots from each vegetation type were selected with replacement, and taxonomic richness (number of taxa) was derived for every taxonomic level. For the temporal accumulation curve, taxonomic richness was counted per season for each vegetation type (total of four seasons per vegetation type). The taxonomic richness of the seasonal data was derived without replacement for each vegetation type. For the spatial and temporal accumulation curve, taxonomic richness was counted per plot, per

season for each vegetation type (total of 60 plots per vegetation type). Then, 60 plots from each vegetation type were selected with replacement and used to derive taxonomic richness (number of taxa) for every taxonomic level. In addition, the spatial and temporal accumulation curves of three mixed vegetation types was calculated to reveal the effect of the loss of a certain vegetation type to the local taxonomic diversity of arthropods; all four possible cases were reconstructed. Taxonomic richness was counted per plot, per season for each vegetation type (total of 60 plots per vegetation type). Then, 180 plots from the three vegetation types were selected with replacement and used to derive taxonomic richness (number of taxa) for every taxonomic level (total 180 plots per accumulation curve).

The effects of environmental factors on mean taxon richness and the abundance (number of individuals) of each taxonomic level (per trap per survey calculated for every plot) were assessed by generalised linear models (GLMs) using the glm.nb function of the MASS library in R (Ripley et al. 2013). Each dependent variable was fitted to a linear predictor:

$\mu \sim \beta_0 + \beta_1 E_1 + \ldots + \beta_7 E_7 +$ offset (O)

where μ was each dependent variable; β_0 was an intercept; $\beta_{1\text{-}7}$ was an estimator of the coefficient of $E_{1\text{-}7}$; $E_{1\text{-}7}$ were seven environmental factors. These environmental factors were standardized to be able to compare the relative importance of each environmental factor. O was the log (number of traps in the plot). The link function of the linear predictor μ was log μ. The error distribution of μ was Poisson for taxon richness, and negative binomial for abundance. The fitness of the constructed models was evaluated based on Akaike's information criterion (AIC: Akaike 1973) and the model with the lowest AIC was selected as the best.

3-3 Results

A total of 3405 ground-dwelling animals were caught in the 1539 trapping days, representing 28 orders of Animalia, 770 individuals of 18 families of Coleoptera, and 448 individuals of 32 species of Carabidae.

Results of the GLMs assessing the relationship between vegetation type and taxonomic diversity are summarised in Table 3-1. At the small spatial scale the model (B+P)(G+L) best explained the variation in order-level taxonomic diversity ($\Delta AIC_{\text{(best-second model)}} = 1.7$ and $\Delta AIC_{\text{(best-null model)}} = 6.6$; $R^2_{\text{best}} = 0.08$; Table 3-1). In this model order richness was lower in evergreen coniferous forest and deciduous broad-leaved forest (B+P) compared to the other vegetation types (G+L) (Fig 3-1). When considering family and species-level richness at the small spatial scale the best model was (G+B+P)(L) ($\Delta AIC_{\text{(best-second model)}} = 1.5$ and $\Delta AIC_{\text{(best-null model)}} = 2.5$, $R^2_{\text{best}} = 0.04$, for family-level; and $\Delta AIC_{\text{(best-second model)}} = 0.9$ and

$\Delta AIC_{(best\text{-}null\ model)}$ = 21.2, R^2_{best} = 0.12 for species-level; Table 3-1). In these models the taxonomic diversity was higher in the deciduous coniferous plantation (L) compared to the other vegetation types (G+B+P) (Fig 3-1). At the large spatial scale the (G+B+P)(L) model best explained the variation in order-level taxonomic diversity ($\Delta AIC_{(best\text{-}second\ model)}$ = 0.2 and $\Delta AIC_{(best\text{-}null\ model)}$ = 1.6; R^2_{best} = 0.45; Table 3-1), with diversity being highest in deciduous coniferous plantation (L) (Fig.3-1). At the family-level of diversity, the (G+B)(P+L) model was the best ($\Delta AIC_{(best\text{-}second\ model)}$ = 1.1 and $\Delta AIC_{(best\text{-}null\ model)}$ = 4.0; R^2_{best} = 0.06; Table 3-1), with grassland and deciduous broad-leaved forest (G+B) having a higher diversity than the coniferous forests (P+L) (Fig.3-1). At the species-level of diversity, the (B+L)(G+P) model was the best ($\Delta AIC_{(best\text{-}second\ model)}$ = 1.9 and $\Delta AIC_{(best\text{-}null\ model)}$ = 10.6; R^2_{best} = 0.30; Table 3-1), with diversity being higher in deciduous broad-leaved forest and deciduous coniferous plantation (B+L) than the rest of vegetation types (G+P)(Fig.3-1).

Taxonomic richness at the order-, family- and species-levels were calculated using four kinds of sample-based accumulation curves; (i) spatial accumulation curves (Fig. 3-2), (ii) temporal accumulation curves (Fig. 3-3), (iii) spatial and temporal accumulation curves (Fig. 3-4), (iv) spatial and temporal accumulation curves of three mixed vegetation types (Fig. 3-5). Spatial accumulation curves of the order-level richness tended to be highest in deciduous coniferous plantations at both small and large spatial scales. Richness of families in the order Coleoptera tended to be highest in grasslands at small spatial scales, and in broad-leaved forests at large spatial scales. Species richness tended to be highest in deciduous coniferous plantations at small spatial scales, and lowest in evergreen coniferous forest at large spatial scales. The temporal accumulation curves of order and family richness tended to increase greatly in deciduous broad-leaved forests (Fig. 3-3). Whereas species richness tended to increase in both grassland and deciduous broad-leaved forest. The spatial and temporal accumulation curves of all three levels of taxonomic richness tended to be highest in deciduous coniferous plantations at the small scale (Fig. 3-4). Whereas at the larger scale, while order richness was also highest in deciduous coniferous plantations, the family- and species-level richness's were highest in deciduous broad-leaved forest. The spatial and temporal accumulation curves of three mixed vegetation types indicated that order richness was lowest in deciduous broad-leaved forests, and both family- and species-level richness's were lowest in grasslands (Fig. 3-5).

Three environmental factors related to soil conditions affected both taxonomic richness and abundance at different taxonomic levels (Table 3-2, 3-3). The soil hardness had a negative effect on taxonomic richness and abundance of all taxonomic levels (Table 3-2, 3-3). The depth of soil A horizon negatively affected the abundance of all taxonomic levels and species richness of the family Carabidae (Table 3-2, 3-3). Soil water content tended to have a negative effect on abundance of the order Coleoptera and the family Carabidae (Table 3-2,

3-3).

3-4 Discussion

Spatial and temporal heterogeneity in ground-dwelling arthropod diversity

This study found varying associations between vegetation types and diversities depending on the spatial and temporal scale examined. The spatial accumulation curves of taxonomic richness showed higher species-level richness in deciduous coniferous plantation than the other three vegetation types when spatial-scale was small (Fig. 3-1 and 3-2). However, because species richness of deciduous coniferous plantation was saturated early with increasing number of plots, species richness became higher in deciduous broad-leaved forest at the larger spatial scale. Family-level richness was highest in grasslands at the small spatial scale, whilst it was highest in broad-leaved forests at the large spatial scale. Order-level richness was highest in deciduous coniferous plantations at the large spatial scale, however the difference with deciduous broad-leaved forests become small with increasing number of plots. The high beta diversity in the broad-leaved forest might be a result of spatial heterogeneity in plant species composition, which possibly leads to heterogeneity in environmental factors as well as bait composition (discussed in the next section).

The temporal (seasonal) heterogeneities in species richness tended to be highest in grasslands (Fig. 3-3), indicating that the community composition of carabid species changes throughout the seasons, especially in grasslands. This result is also consistent with the findings in Chapter 2, where grasslands had the most number of specialists, but no specialist species were shared between the early and late surveys. Seasonal heterogeneity in grasslands is likely due to differences in the timing of reproduction. In this study, we used pitfall traps to collect samples, and the number of individuals sampled depends on their activity, which usually increases in the breeding season (Sota 1985). Grasslands have many herbivorous species (Fig. 2-4), which tend to reproduce in spring, whilst predator species, which inhabit both grasslands and forests, tend to reproduce in autumn (Amazaki et al. 2003). This finding highlights the importance of seasonal heterogeneity in understanding regional biodiversity, although previous studies have only compared taxonomic richness among seasons (Vries et al. 1999; Hawes et al. 2002; Antunes et al. 2008; Donoso et al. 2013).

The diversity of ground-dwelling arthropods in each vegetation type

The contribution of evergreen coniferous forests and deciduous coniferous

plantations to local carabid diversity were lower than grasslands and deciduous broad-leaved forests (Fig. 3-4). Lower levels of carabid beetle species richness in evergreen coniferous plantation compared to deciduous broad-leaved natural forest is a well-known pattern (e.g. Fahy & Gormally, 1998; Fuller et al. 2008; Magura et al. 2003). However, only a limited number of studies have compared carabid beetle species richness between deciduous broad-leaved natural forests and deciduous coniferous plantations, in one case showing that it was higher in the natural forest than the plantation (Yu et al. 2006), and in another that there was no difference between the two forest types (Yu et al. 2008). The results of this study are in accordance with Yu et al. (2006). The low contributions of the two types of coniferous forest to species diversities in this study can be attributed to the effect of coniferous monoculture and the characteristics of the environmental factors found there (described below). Lower levels of species richness in plantations compared to natural forests have often been found in Europe (Fahy and Gormally 1998; Fuller et al. 2008; Magura et al. 2003), but may be attributed to the mixed effect of afforestation and cover type.

GLMs and accumulation curves showed that order- and family-level richness were lowest in evergreen coniferous natural forest. Previous studies reported that the species richness of the orders Acarina, Collembola, Araneae, and Coleoptera, as well as the Staphylinidae family, is higher in deciduous broad-leaved natural forests than evergreen coniferous plantations (Cakir and Makineci 2013; Schuldt and Assmann 2011; Vásquez-Vélez et al. 2010; Wiezik et al. 2007); and the species richness of arthropods is higher in grasslands than evergreen coniferous plantations (Pryke and Samways 2011). Similar to the species-level diversity of the family Carabidae, the low taxonomic richness of the family- and order-levels in evergreen coniferous natural forests could be due to cover type (i.e. evergreen and conifer) or other environmental factors. The contributions of grasslands to local order-level diversity was also low, due to the low abundance of Gastropoda, most species of which require a high volume of litter and fallen tree trunks to live. The comparison of family richness between deciduous broad-leaved forests and deciduous coniferous plantations indicated that both the accumulated and total taxonomic richness were higher in deciduous broad-leaved natural forests. These findings are supported by the report that species richness of the order Coleoptera (Wiezik et al. 2007) and the families Curculionidae and Staphylinidae (Ohsawa 2005; Luo et al. 2013) were higher in deciduous broad-leaved natural forests than deciduous coniferous plantations. The low diversities in the two types of coniferous forests might be caused by the effect of monoculture. The enemies hypothesis states that a higher species richness of plants maintains a higher diversity of predators (Root 1973). Indeed, herbivorous arthropods tend to eat specific species of plants, thus a low-level of plant species diversity, such as in coniferous monocultures, would not be able to host a high diversity of arthropods. Moreover, the heterogeneity in plant species composition, which leads to heterogeneity in

environmental factors as well as bait composition. For example, leaf litter nutrient quantities differ among species of broad-leaved trees (Emmer et al. 1998), and soil nutrients and pH differ between pioneer and other types of trees (Saure et al. 2013).

The effects of environmental factors on ground-dwelling animal diversities

Three environmental factors were found to affect taxonomic richness and/or the abundance of all taxonomic levels. The soil hardness had a negative effect on taxonomic richness and the depth of soil A horizon also had a negative effect on the abundance of soil-dwelling animals. The negative effects of soil hardness on carabid beetle species richness and abundance have been previously reported (Cole et al. 2002; Magura 2002; Magura et al. 2003). Under the hard soil surface, soil-dwelling animals might not be able to use sufficient nutritional and spatial resources and the abundance of predators also decreases. In this study, the soil hardness was lowest in deciduous coniferous plantations (Fig. 2-6), and may have increased the species richness of carabid beetles at small spatial scales. Nojima et al. (2013) observed that the diversity of ground dwelling animals (the Arachnid and Centipede classes, and the Coleoptera and Isopod orders) was higher in plots where the soil A-horizon was shallower. In this study, the deepest soil A horizon was in evergreen coniferous natural forests (Fig. 2-6), and this may have contributed to the decreased taxonomic richness and abundance of soil-dwelling animals observed in this vegetation type. Although the coverage of dwarf bamboo did not have any effect on the taxonomic richness and abundance of arthropods, Ueda et al. (2009) reported that the abundance of two carabid beetle species (which were also captured in this study) were negatively affected by the abundance of dwarf bamboo. Indeed, data from this study also suggests that the coverage of dwarf bamboo tended to alter the community composition of carabid beetle species (Table 2-4), although further studies are required.

Tables of Chapter 3

Table 3-1 Akaike's information criterion (AIC) values of compared generalized linear models (GLMs) for the effects of vegetation type on order richness of the kingdom Animalia, family richness of the order Coleoptera, species richness of the family Carabidae summed for each plot for small scale, and each vegetation type for large scale in each vegetation type. AICs of the selected models, on which Figs. 3-1 is based, are in bold. Parentheses of models indicate vegetation group(s) whose effects were differently estimated from other vegetation group(s). G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation.

Model	Order richness		Family richness		Species richness	
	Small scale	Large scale	Small scale	Large scale	Small scale	Large scale
(G+B+P+L)	652.3	252.6	434.9	235.4	435.2	229.8
(B+P+L)(G)	650.5	254.5	436.6	236.1	429.9	228.3
(G+B+L)(P)	649.8	252.3	436.8	232.7	434.9	226.6
(B)(G+P+L)	652.5	254.2	435.0	234.8	436.2	228.7
(G+B+P)(L)	652.4	**251.0**	**432.4**	236.9	**414.0**	227.0
(B+L)(G+P)	654.3	253.4	436.4	236.8	424.5	**219.4**
(G+B)(P+L)	654.0	254.4	434.1	**231.4**	427.2	231.8
(B+P)(G+L)	**645.7**	251.2	435.0	237.3	432.5	231.7
(B)(G+P)(L)	653.6	253.0	433.9	236.8	415.3	221.3
(G+B)(L)(P)	651.3	252.2	434.1	232.5	416.0	226.2
(B)(G+L)(P)	647.4	252.9	436.5	233.7	434.4	227.4
(B+L)(G)(P)	650.1	254.3	438.4	234.4	426.0	221.3
(B)(G)(P+L)	652.0	256.2	435.8	233.3	428.0	228.9
(B+P)(G)(L)	647.6	252.2	434.4	238.0	414.9	227.6
(B)(G)(L)(P)	649.3	253.9	435.9	234.4	416.8	223.2

Table 3-2 Akaike's information criterion (AIC) values of compared generalized linear models (GLMs) for the effects of seven environmental factors on order richness of the kingdom Animalia, family richness of the order Coleoptera, species richness of the family Carabidae, and abundance of each taxonomic level, assuming negative binomial and Poisson distribution for abundance and taxonomic richness, respectively. AIC values of the selected models are from Table 3-1. DF is residual degree of freedom. + indicates the variable is included in the model.

		Intercept	Canopy gaps	Coverage of bamboo grass	Soil porosity	Soil water content	Soil hardness	Depth of soil horizon A	Litter depth	DF	AIC
Order richness	Best model	1.55					+			2	479.5
	Second model	1.55					+	+		3	479.8
	Null model	1.55								1	484.0
Abundance	Best model	2.64					+	+		4	831.8
	Second model	2.64	+				+	+		5	832.3
	Null model	2.67								2	842.1
Family richness	Best model	0.21					+			2	318.9
	Second model	0.20		+			+			3	319.7
	Null model	0.22								1	321.4
Abundance	Best model	1.15				+	+	+		5	556.7
	Second model	1.16	+			+	+			5	557.8
	Null model	1.28								2	572.4
Species richness	Best model	-0.11				+	+	+		4	310.3
	Second model	-0.10				+	+			3	311.0
	Null model	-0.02								1	323.7

	Best model	0.62		+	+		4	446.8
Abundance	Second model	0.60		+	+	+	5	447.4
	Null model	0.82					2	462.5

Table 3-3 Effects of seven environmental factors on order richness of the kingdom Animalia, family richness of the order Coleoptera, species richness of the family Carabidae, and abundance of each taxonomic level. R^2 values analyzed by generalized linear models (GLMs) assuming Poisson and negative binomial distribution for taxonomic richness and abundance, respectively.

		Canopy gaps	Coverage of bamboo grass	Soil porosity	Soil water content	Soil hardness	Depth of soil horizon A	Litter depth	R^2 value
Animalia	Order richness	-	-	-	-	-0.11 *	-	-	0.07
	Abundance	-	-	-	-	-0.22 ***	-0.13 *	-	0.05
Coleoptera	Family richness	-	-	-	-	-0.14	-	-	0.05
	Abundance	-	-	-	-0.18	-0.39 ***	-0.39 **	-	0.13
Carabidae	Species richness	-	-	-	-	-0.32 ***	-0.43 ***	-	0.13
	Abundance	-	-	-	-0.30	-0.34 *	-0.44 **	-	0.15

Estimated effects of selected variables in the best model based on Akaike's information criterion (AIC; Table 3-2) and the significance level of each variable by the Wald test (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$) are shown. Residual degree of freedoms of each model was 167.

Figures of Chapter 3

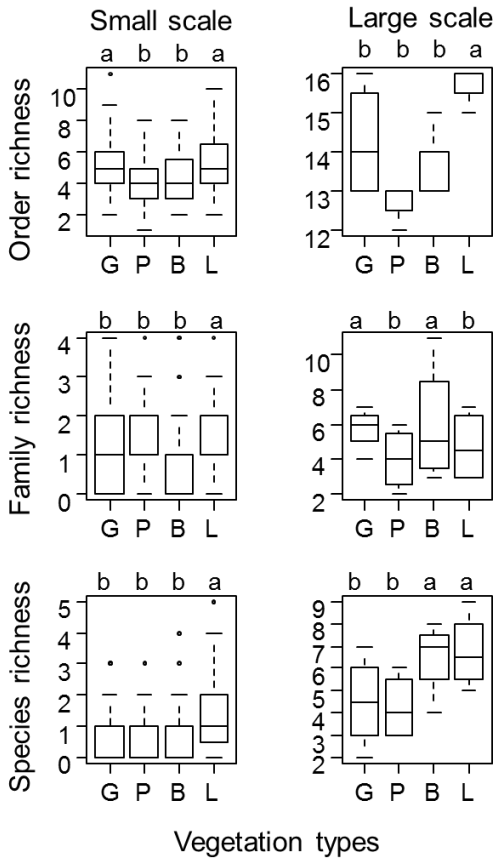

Fig. 3-1 Box plots of the taxonomic richness of: orders (of all animals), families (of Coleoptera) or species (of Carabidae), summed for each plot for small scale, and each vegetation type for large scale in each vegetation type. Vegetation types with different letters have significantly different means, according to the model selection using generalized linear models (GLMs). The boxes indicate the lower quartile, median, and upper quartile. The whisker lines extend from lower quartile − 1.5 × interquartile range (IQR) to upper quartile + 1.5 × IQR. Dots represent data points beyond the ends of the whiskers. G: grassland, P: evergreen coniferous *Pinus* forest, B: deciduous broad-leaved forest, and L: deciduous coniferous *Larix* plantation.

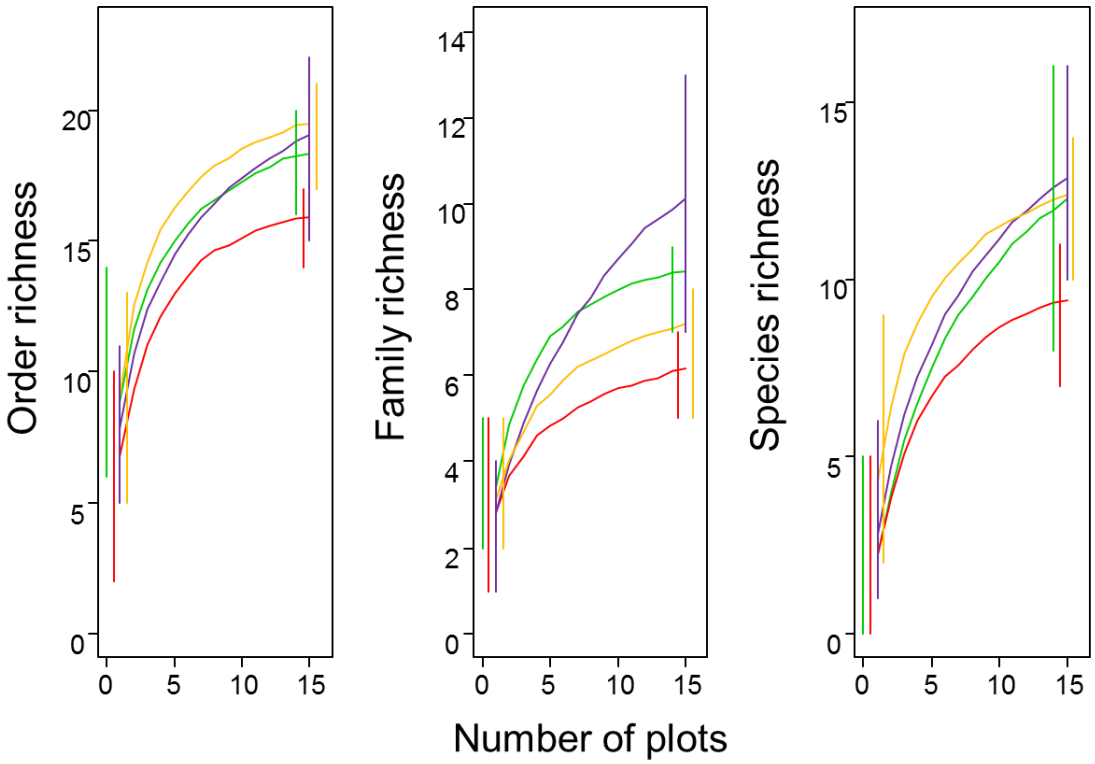

Fig. 3-2 Spatial accumulation curves of ground-dwelling animals; order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae, resampled from 15 plots of each vegetation type using the mean number of shared taxa in four surveys. Vertical lines mean 95% confidence intervals. Green lines: grassland, red lines: evergreen coniferous *Pinus* forest, purple lines: deciduous broad-leaved forest, yellow lines: deciduous coniferous *Larix* plantation.

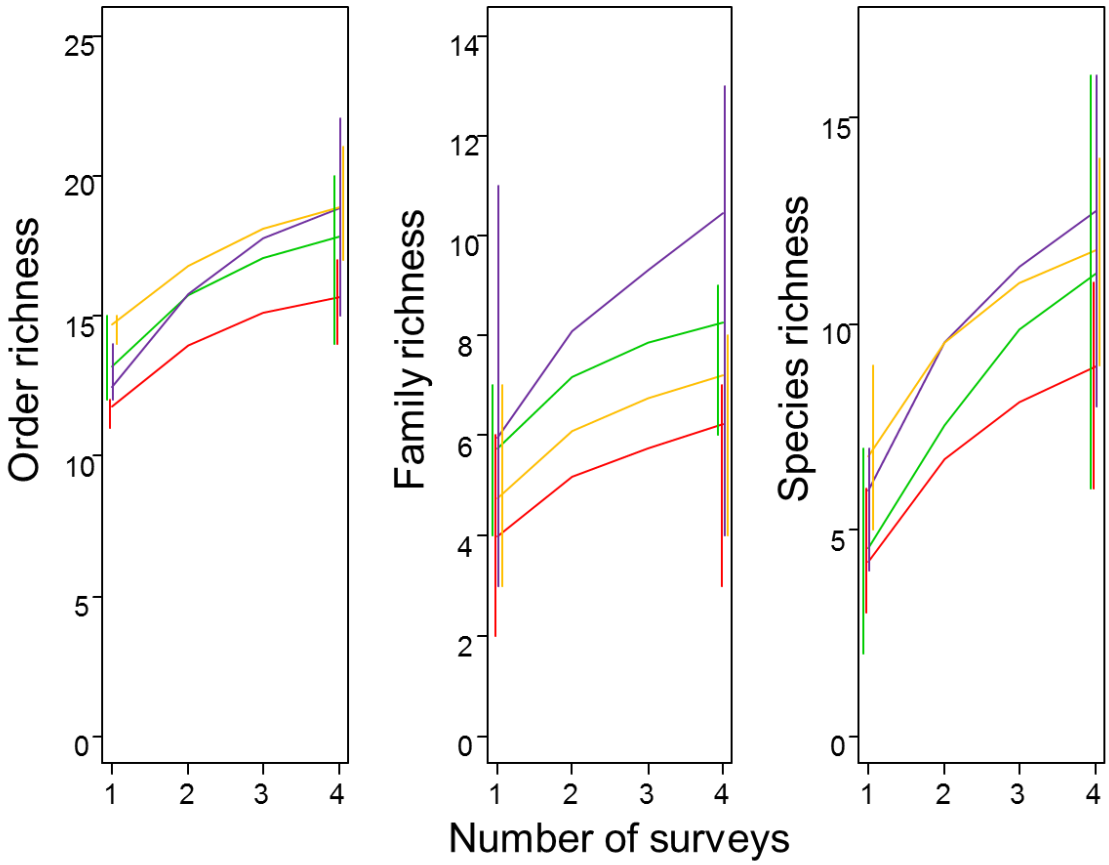

Fig. 3-3 Temporal (seasonal) accumulation curves of ground-dwelling animals; order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae, resampled at four surveys from each vegetation type using the mean number of shared taxa in 15 plots. Vertical lines mean 95% confidence intervals. Green lines: grassland, red lines: evergreen coniferous *Pinus* forest, purple lines: deciduous broad-leaved forest, yellow lines: deciduous coniferous *Larix* plantation.

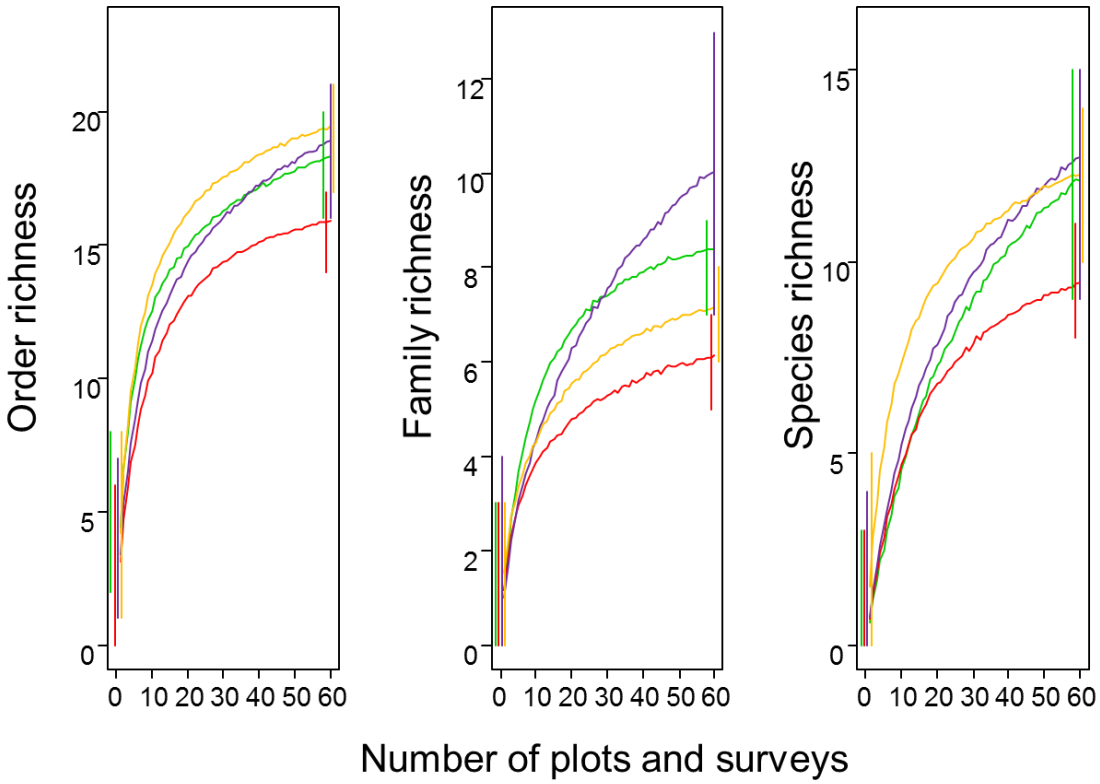

Fig. 3-4 Spatial and temporal accumulation curves of ground-dwelling animals; order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae, resampled at 60 plots from each vegetation type using the mean number of shared taxa in each survey. Vertical lines mean 95% confidence intervals. Green lines: grassland, red lines: evergreen coniferous *Pinus* forest, purple lines: deciduous broad-leaved forest, yellow lines: deciduous coniferous *Larix* plantation.

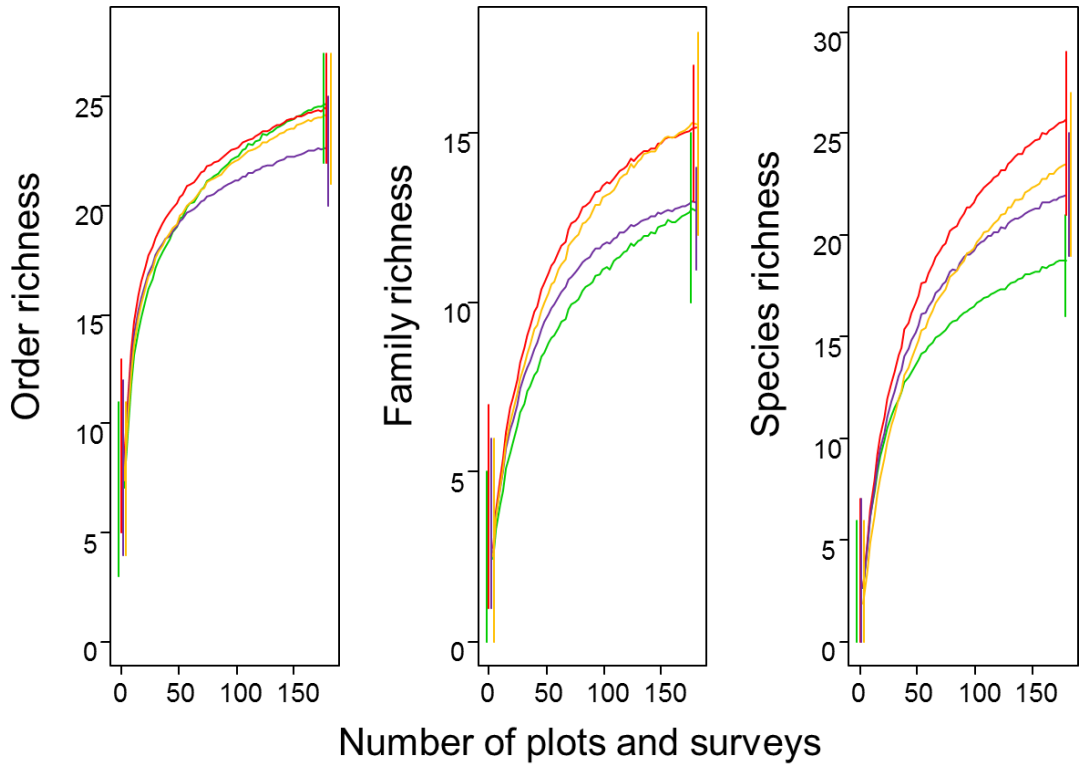

Fig. 3-5 Spatial and temporal accumulation curves (three mixed vegetation types) of ground-dwelling animals; order-level of Animalia, family-level of order Coleoptera, and species-level family Carabidae, resampled at 180 plots from three vegetation types using the mean number of shared taxa in each survey. Vertical lines mean 95% confidence intervals. Green lines: grassland, red lines: evergreen coniferous *Pinus* forest, purple lines: deciduous broad-leaved forest, yellow lines: deciduous coniferous *Larix* plantation.

Chapter 4:
The effect of landslides on the diversity and community composition of epigeic and subterranean arthropods.

4-1 Introduction

The role of natural disturbances in creating and maintaining biodiversity has been a central issue in ecology (e.g. Connell 1978; Townsend et al. 1997; Mayor et al. 2012). This chapter focused on the effect of one type of natural disturbance, landslides,, on the diversity and community composition of arthropods. Landslides increase regional biodiversity by providing heterogeneity in vegetation types, soil quality and landscapes such as cliffs and marshes (Geertsema and Pojar 2007; Walker and Shiels 2013). Japan has a high occurrence of landslides due to active crustal movement and high precipitation (Hong et al. 2007). In addition, landslides are known habitats for subterranean arthropods (e.g. Culver and Pipan 2008), a faunal group often used as bioindicators in diversity surveys and monitoring programs. Subterranean fauna was first discovered in caves in the late 18th century (Laurenti 1768), and since then have also been collected in between soil B and C layers, called Mesovoid Shallow Substratum (MSS) (Juberthie et al. 1980; Gers and Dupuis 1988). Recently, many new species of subterranean arthropods, often with degenerated eyes or body pigment, have been discovered in shallow subterranean habitats (SSH) of landslide areas (Culver and Pipan 2008; Ito 2010; Barranco et al. 2013; Sugaya and Yamasako 2014; Olmi et al. 2014).

So far, no studies have quantitatively examined the effect of landslides on the abundance, diversity, and community composition of arthropods, due to two methodological shortcomings. Firstly, limited replications have not enabled sufficient statistical analyses. For example, Rendoš et al. (2012) and Nitzu et al. (2014) investigated only one or two sites, and one hole per site. Secondly, these previous studies did not compare the diversities and communities of arthropods between landslide areas and undisturbed control areas. Although Rendoš et al. (2012) and Nitzu et al. (2014) suggested that soil depth, season, and altitude affect arthropod communities in landslide areas, those effects were not separated from the effect of treatment (i.e. landslide area vs. undisturbed area) or environmental factors (i.e. ground surface vs. underground). The lack of comprehensive studies of the animal communities associated with landslides is in contrast to plant studies; plant community compositions are reported to be different between landslide and undisturbed areas, probably due to soil moisture (Nakamura 1984; Huck et al. 2013).

Differences in some environmental factors between landslides and undisturbed areas could possibly affect arthropod communities. For example, in the SSH of landslide areas, the abundant rocks will increase habitat space for arthropods. In addition, annual fluctuations in temperature and humidity in subterranean landslide areas are less extreme than at the surface (Pipan et al. 2010; Nitzu et al. 2014), perhaps making these habitats suitable for soil fauna with limited dispersal ability. Thus, these environmental factors might help to maintain high taxonomic richness and abundance of arthropods. Finally, it is predicted that arthropod communities contain more endemic taxa in landslide areas than in undisturbed areas, due to the low dispersal ability of subterranean fauna and specialization on the landslide environment.

This chapter studied arthropod communities in landslide and undisturbed areas of mountain regions in order to address three questions: i) whether the abundance (number of individuals) and diversity of arthropods are higher in landslide areas than undisturbed areas, ii) whether landslide areas have characteristic community compositions, including endemic taxa, and iii) which taxonomic groups are indicators for landslide and underground habitats.

4-2 Material and Methods

Study sites and sample collection

Samples were collected in four mountain regions in central Japan's cool-temperate zone: Joshin'etsu highland, Mt. Yatsugatake, the South Japanese Alps and Mt. Chichibu (Fig. 4-1). Two or three landslide areas were chosen in each region (total 11 landslides, Table 4-1). At each landslide six holes were dug within the landslide (> 2 m between holes) and three holes in undisturbed areas near each landslide (< 30 m from each landslide) as control. In each hole, traps were set at each of 0, 25 and 50 cm depth from the ground surface (total 258 traps). The traps used were those devised by Nishikawa et al. (2012) and also used in Hayashi, Ogai, and Nagasawa (2015). The traps consisted of a bait container and an inner cup (Fig. 4-2). The bait container contained 30 g of minced dry silkworm chrysalis with 30 ml of 5% potassium sorbate as preservative. The trap lid had a 20 mm wide entrance. The inner cup contained 50 ml of 50% propylene glycol as a preserving agent for collected insects. Traps were set during August and September in 2014 and collected 36 – 70 days later. All arthropods larger than 1 mm in body length were identified to order following Aoki (2015). All arthropods in the orders Hymenoptera, Grylloblattodea, Diplura, Araneae, Chilopoda, Diplopoda, Pseudoscorpionida, and Coleoptera were identified to families and a part of them to species level. These identifications were conducted by Mr. Y. Chikami, Dr. T. Mita, Dr. M. Yamane, Mr. T. Suguro, Dr. T. Uchifune, Mr. H. Ohira, Dr. K. Sekiya, Mr. N. Ito, Dr. M. Ohara, Mr. Y. Sawada, Dr. Y. Hayashi, and Dr. S. Nomura.

Statistical analyses

To examine the effect of landslides, the abundance (number of individuals) of all collected arthropods, and taxon richness of each taxonomic level (order-level of all arthropods and family- and species-levels for the orders Hymenoptera, Grylloblattodea, Diplura, Araneae, Chilopoda, Diplopoda, Pseudoscorpionida, and Coleoptera) per trap were assessed by negative binomial regression in generalized linear models (GLMs) and Poisson regression in generalized linear mixed models (GLMMs), respectively. Each dependent variable was fitted to a linear predictor:

$\mu \sim \beta_0 + \beta_1 T + \beta_2 D + \beta_3 T{:}D + R$

where μ was each dependent variable; β_0 was an intercept; $\beta_{1\text{-}3}$ were an estimator of the coefficients of *T; T* was categorical factor, which was either landslide or undisturbed area*; D* was depth of each trap; *T:D* was the interaction of *T–D*; and *R* was a random effect of studied regions, which was either Joshin'etsu highland, Mt. Yatsugatake, the South Japanese Alps, or Mt. Chichibu (only used for taxon richness analyses). The link function of the linear predictor μ was log μ. The error distributions of μ were negative binomial and Poisson, for the abundance and taxon richness analyses respectively. The glm.nb function of the MASS library (Ripley et al. 2013) and glmer function of the lme4 library (Bates 2008) in *R* ver. 2.15.1 (*R* Core Team 2012) were used for abundance and taxon richness analyses, respectively. The fitness of all the constructed models was evaluated based on Akaike's information criterion (AIC) and the model with the lowest AIC was selected as the best.

To assess arthropod community composition, a data set of the mean abundance of each taxon per depth, per trap, per treatment (landslide or undisturbed area) calculated for every site was used. The effects of treatment (landslide or undisturbed area), as well as depths of traps, regions and their interactions, on the calculated order-level community composition of all arthropods and family- and species-level community compositions of the orders Hymenoptera, Grylloblattodea, Diplura, Araneae, Chilopoda, Diplopoda, Pseudoscorpionida, and Coleoptera, were analyzed by permutational multivariate analysis of variance (PERMANOVA: Anderson 2001) using the adonis function in the vegan library (Oksanen et al. 2015) with the Horn–Morisita index and 9,999 permutations and all other default settings. An interaction between treatment and regions was detected, therefore the data set was divided into landslide and undisturbed areas and PERMANOVA repeated on each treatment separately to isolate the effect of treatment on community composition.

If the PERMANOVA indicated that treatments (landslide or undisturbed area) and depth of traps affected the arthropod community, the dataset was split in a hierarchical manner, first creating two classes of treatments, landslide and undisturbed area, then further classifying the three depths of traps. Then to identify taxa that characterized the arthropod community in landslide or undisturbed area and each depth (0, 25, and 50 cm) and to understand the effect of landslide more specifically, the indicator value test (IndVal, Dufrene and Legendre 1997) was conducted to classify almost all collected arthropods into these eight classes of treatment and depth. The resulting indicator values were tested for significance using a randomization test (9,999 times). The IndVal test was conducted using the indval function in the labdsv library (Roberts 2015) in *R*.

4-3 Results

A total of 7865 arthropods from 19 orders were collected, including 32 families and 106 species of Hymenoptera, Grylloblattodea, Diplura, Araneae, Chilopoda, Diplopoda,

Pseudoscorpionida, and Coleoptera.

The landside areas had higher arthropod abundance and order richness than undisturbed areas ($\Delta AIC_{(best\text{-}second\ model)}$ = 20.9 and 1586.3 and $\Delta AIC_{(best\text{-}null\ model)}$ = 1.5 and 41.1, and R^2_{best} = 0.23 and 0.23 for arthropod abundance and order richness, respectively, Table 4-2 and Table 4-3). The soil depth had a negative effect on the abundance and taxon richness (order, family and species), because the differences in AIC values between the best model and the model that did not contain the effect of depth were 1337.3, 30.3, 50.2, and 45.2 for abundance, order richness, family richness, and species richness, respectively (Table 4-2) and the soil depth had negative coefficients for all analyses. Family and species richness were affected by the interaction of depth and treatment ($\Delta AIC_{(best\text{-}second\ model)}$ = 0.8 and 68.2 and $\Delta AIC_{(best\text{-}null\ model)}$ = 1.5 and 57.0, and R^2_{best} = 0.23 and 0.10 for family- and species-level, respectively; Table 4-2 and Table 4-3), showing a gentler slope of the taxon richness along depth in landslide areas (Fig. 4-3).

Three independent variables (treatment, depth, region; and interactions of depth–treatment, region–treatment, and region–depth) significantly affected arthropod community composition (PERMANOVA; Table 4-4). Region contributed most to the variation in arthropod community composition at all taxonomic levels. The interaction of region and treatment had the second highest contribution (Table 4-4) with the effect of region tending to be higher in landslide areas compared to undisturbed areas in all taxonomic levels (PERMANOVA; Table. 4-5). Depth and treatment also contributed significantly to order- and species-level, and family-level community composition, respectively (Table 4-4).

The IndVal test detected two families [Braconidae (Hymenoptera) and Histeroidea (Coleoptera)] and two species [*Pterostichus spiculifer* and *P.* sp. 1 (Coleoptera: Carabidae)] as significant indicators of landslide area (Fig. 4-4). Significant indicators of soil depth in landslide areas were also detected in most cases. In order and family level, Dermaptera, Chordeumatida, Liocranidae (Araneae), and Diplomaragnidae (Chordeumatida) and Grylloblattodea and Grylloblattidae (Grylloblattodea) were significant indicators of 0 cm and 50 cm soil depth in landslide area, respectively (Fig. 4-4). In species level, *Formica japonica* (Hymenoptera: Formicidae) and *Dinotrema* sp. 1 (Hymenoptera: Braconidae), *Galloisiana yuasai* (Grylloblattodea: Grylloblattidae), and *Colpodes kyushuensis* (Coleoptera: Carabidae) were significant indicators of 0 cm, 25 cm, and 50 cm soil depth in landslide area, respectively (Fig. 4-4).

4-5 Discussion

Distribution of taxon diversity and abundance

During the sampling for this study many undescribed species were discovered, mainly

from the Coleoptera and Hymenoptera. Among them collaborators and I reported *Sciaphyes japonicas* [Coleoptera: Leiodidae: Leptodilini; (Hayashi et al. 2015)] and *Pterostichus nagasawai* [Coleoptera: Carabidae: Pterostichini; (Ito and Ogai 2015)] as new species. Recently, many new species of arthropods in orders such as Coleoptera, Hymenoptera and Orthoptera have been found in the underground habitats of landslide areas (Ito 2010; Faille et al. 2012; Ito 2012; Barranco et al. 2013; Sugaya and Yamasako 2014; Olmi et al. 2014; Ortuño et al. 2014). These studies suggest that many unknown species still exist in landslide areas.

This study revealed that landslide areas had a higher arthropods abundance and order level diversity than undisturbed areas and the depth below ground surface negatively affected diversity and abundance (Table 4-2, 4-3, Fig. 4-3). Although previous studies have suggested high levels of diversity and abundance of arthropods in landslide areas (Rendoš et al. 2012; Nitzu et al. 2014), control sites (undisturbed area) were not included and there were few traps and study sites. Arthropod diversity decreased with the increase in depth from ground surface (Table 4-3). This pattern has also been found in previous studies (Laška et al. 2011; Rendoš et al. 2012; Nitzu et al. 2014). In addition, this study found that the decrease in family and species richness with depth was less pronounced in landslide areas (Fig. 4-3). One possible explanation is that the diversity of morphologically typical subterranean arthropods was higher in the deeper soil of landslide areas (Nagasawa unpublished data). There are more cracks in the SSH of landslide areas than in undisturbed areas, which may provide habitats for arthropods. In addition, temperature and humidity are constant throughout the year in the SSH of landslide areas (Pipan et al. 2010; Nitzu et al. 2014), and may provide a suitable environment for arthropods with limited dispersal abilities.

Indicators of landslide habitats and soil depth

More than half of species and more than one third of orders and families depended on the landslide areas (Fig. 4-4). Grylloblattidae was selected as an order-level indicator of landslide areas at 50 cm soil depth. This order is known to prefer cool and moist microenvironments (Schoville 2010) and have degenerated eyes, body color, and wings. Braconidae (Hymenoptera) and Histeroidea (Coleoptera) were selected as family-level indicators of landslide areas. Braconidae are a large family of parasitoid wasps and some of the species that were collected in this study have degenerated wings and eyes. In general, Histeroidea has hind-wings and flight ability, but in this study, most of the Histeroidea were from the genus *Anapleus* and had degenerated hind-wings and body colors. The order Grylloblattidae and a part of the families Braconidae and Histeroidea might be specialised subterranean arthropods because of their degenerated eyes or body color. In contrast, *Cordyceps kyushuensis* (Coleoptera: Carabidae), a species with degenerated eyes but hindwings and flight ability, was selected as a significant species-level indicator of 50 cm soil depths in landslide areas. It is very rare for a subterranean arthropod to possess flight ability, so perhaps the species only

temporarily uses the underground habitat, e.g. during a certain season or under specific conditions. Nitzu et al. (2014) also predicted some carabid beetles enter the MSS and screes and use them as a refuge when the outside temperature increases and soil relative humidity decreases. In general the findings of this study support previous studies which have suggested that subterranean arthropods prefer the SSH of landslide areas (e.g. Culver and Pipan 2008).

Endemic community compositions

Because the interaction of region–treatment affected the community compositions (Table 4-4) and the effect of region tended to be higher in landslide area than undisturbed area (Table. 4-5), the community compositions of arthropods were more indigenous in landslide area. Immigration among adjacent regions plays an important role in shaping community composition (MacArthur and Wilson 1967). The environmental conditions of landslide areas are significantly different to undisturbed areas (i.e. litter depth, coverage of vegetation, etc.; Gers 1998; Pipan et al. 2010b), therefore it might be difficult for arthropods to immigrate from one area to the other, isolating and altering community composition in landslide areas. As discussed above, a number of arthropods preferred landslide areas (Fig. 4-4), and most subterranean arthropods, except rare cases such as *Cordyceps kyushuensis*, are flightless and might have low dispersal abilities. Thus, they prefer landslide areas and the SSH and have a limited spatial range. Therefore, isolation in and adaptation to landslide areas or the SSH could promote allopatric speciation, and create endemic community compositions. This prediction is supported by previous molecular phylogenetic studies in Europe (Culve 1970; Crouau-Roy 1986; Faille et al. 2007), where the opportunity for the development of multiple isolated local populations lead to allopatric speciation of subterranean carabid beetles.

The results of this study indicate that the environmental axis of landslides contributes significantly to local arthropod diversity and suggests that a mixed landscape consisting of landslides and undisturbed areas helps to maintain a high biodiversity of arthropods. I found new indicators of the landslide axis and will help promote efficient environmental evaluation.

Tables of chapter 4

Table 4-1 Details of the11 study sites.

Code	Collecting site				N	E	Altitude
	Region	Prefecture	City	Local			(m)
S1	Joshin'etsu highland	Nagano	Suzaka	Mt. Hashigoyama	36.56981	138.35441	1230
S2	Joshin'etsu highland	Nagano	Suzaka	Ôyafudô	36.56317	138.36408	1287
S3	Joshin'etsu highland	Nagano	Ueda	Mt. Kokuzô	36.41118	138.30314	587
S4	Mt.Yatsugatake	Nagano	Minamisakugun	Gokô bokujô campsite	35.94155	138.49048	1343
S5	Mt.Yatsugatake	Nagano	Minamisakugun	Yatsugatake Forest, the Univ. of Tsukuba	35.92556	138.50524	1597
S6	Mt. Chichibu	Saitama	Chichibu	Chichibu Forest, the Univ. of Tokyo	35.93789	138.80548	1186
S7	Mt. Chichibu	Saitama	Chichibu	Chichibu Forest, the Univ. of Tokyo	35.94070	138.80949	1129
S8	Mt. Chichibu	Saitama	Chichibu	Chichibu Forest, the Univ. of Tokyo	35.94055	138.81323	1099
S9	The South Japanese Alps	Shizuoka	Shizuoka	Ikawa Forest, the Univ. of Tsukuba	35.34713	138.22789	1160
S10	The South Japanese Alps	Shizuoka	Shizuoka	Ikawa Forest, the Univ. of Tsukuba	35.34654	138.22982	1148
S11	The South Japanese Alps	Shizuoka	Shizuoka	Ikawa Forest, the Univ. of Tsukuba	35.32543	138.22626	1144

Table 4-2 Akaike's information criterion (AIC) values of compared generalized linear models (GLMs) and generalized linear mixed models (GLMMs) assuming negative binomial and Poisson distribution for abundance and taxonomic richness, respectively. AIC of the selected models, on which Table 4-3 are based, are in bold. DF means residual degree of freedom. + means the variable is included in the model.

	Intercept	Depth (cm)	Treatment	Depth:Treatment	DF	AIC
Abundance of all arthropods	3.73		+	+	5	**5331.5**
	3.64	+	+		4	5352.4
	3.91			+	4	5387.0
	3.91	+			3	5579.6
	3.15		+		3	6668.8
	3.41				2	6917.8
Order richness	1.37	+	+		4	**826.5**
	1.41	+	+	+	5	828.0
	1.55			+	4	828.9
	1.55	+			3	836.2
	1.11		+		3	856.8
	1.29				2	867.6
Family richness	1.30			+	4	**811.9**
	1.21		+	+	5	812.7
	1.03	+	+		4	817.2
	1.30	+			3	833.8
	0.69		+		3	862.1
	0.95				2	880.1
Species richness	0.94	+		+	4	**919.7**
	0.89		+	+	5	921.2
	0.70	+	+		4	927.6
	0.94	+			3	939.4
	0.40		+		3	964.9
	0.64				2	976.7

Table 4-3 Effects of three independent variables on abundance (number of individuals) of all arthropods and taxonomic richness of each taxonomic level analyzed by generalized linear models (GLMs) and generalized linear mixed models (GLMMs) assuming negative binomial and Poisson distribution for abundance and taxonomic richness, respectively. Estimated effects of selected variables in the best model based on Akaike's information criterion (Table 4-2). The random effect of studied regions (Sugadaira highland, Mt. Yatsugatake, the South Japanese Alps, and Mt. Chichibu) was used for taxonomic richness analyses.

	Depth (cm)	Treatment	Depth: Treatment
		Landslide area	Landslide area
Abundance of all arthropods	-0.026 ***	0.258 ***	-0.019 ***
Order richness	-0.010 ***	0.256 ***	—
Family richness	-0.025 ***	—	0.015 ***
Species richness	-0.028 ***	—	0.016 ***

Table 4-4 Effects of three environmental factors on the community composition by permutational multivariate analysis of variance (PERMANOVA) using the Horn–Morisita index of dissimilarity. The R^2 values and the levels of significance are shown, *** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 9,999 permutations.

Taxonomic-level	Treatment	Depth (cm)	Region	Depth: Treatment	Region: Treatment	Region: Depth
Order	0.080 **	0.028	0.231 **	0.026	0.084 *	0.061
Family	0.027	0.018	0.205 **	0.034 *	0.153 **	0.044
Species	0.024	0.056 **	0.219 **	0.022	0.085 *	0.047

Table 4-5 Effects of two environmental factors on the community composition by permutational multivariate analysis of variance (PERMANOVA) using the Horn–Morisita index of dissimilarity. The R^2 values and the levels of significance are shown, *** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 9,999 permutations.

Taxonomic-level	Depth (cm)		Region		Region:Depth	
	Landslide area	Undisturbed area	Landslide area	Undisturbed area	Landslide area	Undisturbed area
Order	0.097 **	0.080 **	0.400 **	0.234 **	0.199 *	0.062
Family	0.033	0.082 **	0.500 **	0.231 **	0.070	0.114
Species	0.049 *	0.036	0.340 **	0.274 **	0.098	0.129 *

Figures of chapter 4

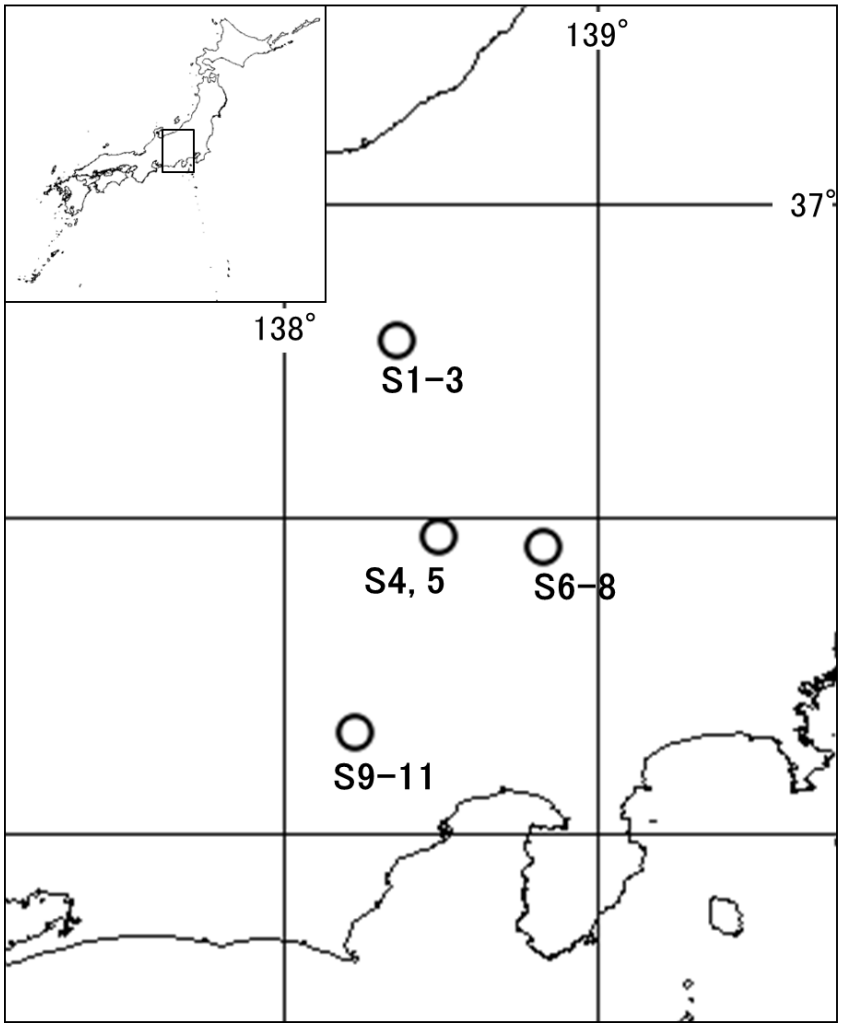

Fig. 4-1 The location of study sites. The numbers of the study sites correspond to those in Table 4-1.

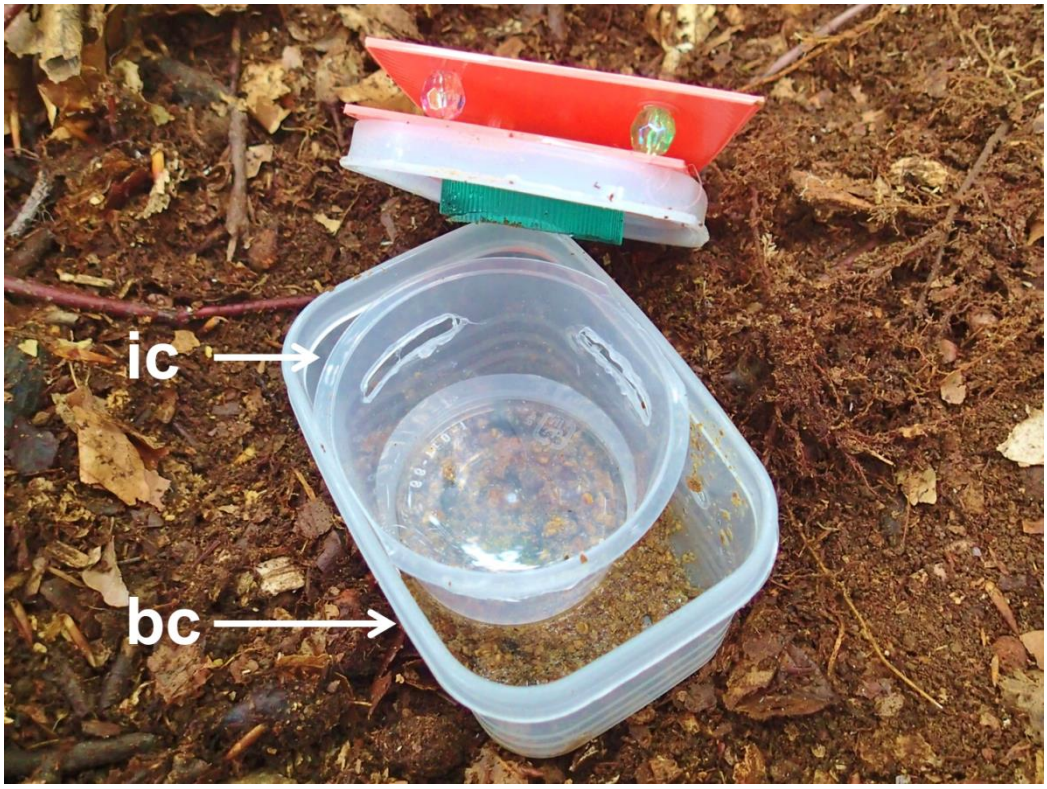

Fig. 4-2 The structure of the baited deep-soil trap; bc: a bait container and ic: an inner cup.

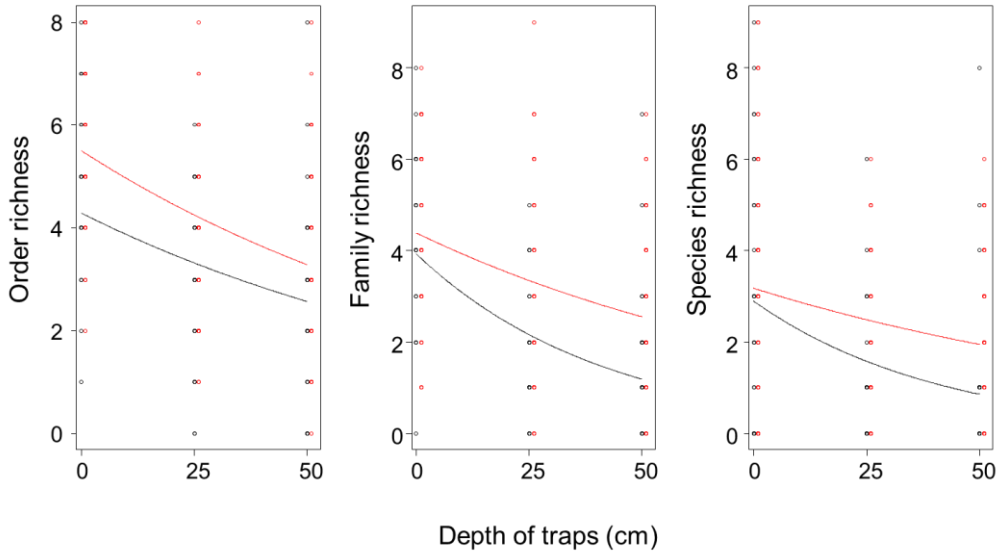

Fig. 4-3 The estimated taxonomic richness of each taxonomic level using generalized linear mixed models (GLMMs). The lines and the dots indicate the estimated taxonomic richness and observed values, respectively. Red indicates landslide areas and black indicates undisturbed areas.

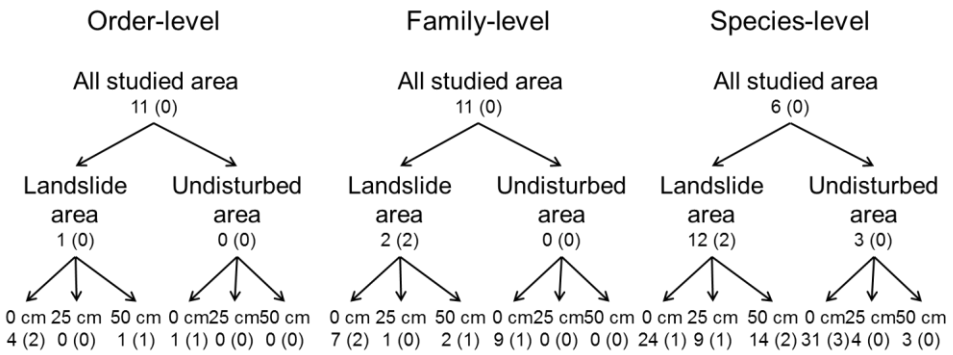

Fig. 4-4 Tree diagram of the landslide and undisturbed area with the associated numbers of indicator taxa for each taxonomic level. 0, 25, 50 cm means the depth of the trap below the surface calculated by the indicator value test (IndVal, Dufrene and Legendre 1997). The numbers in parentheses are significant indicator taxa ($P < 0.05$; 9,999 permutations).

General Discussion

The chapters of this thesis revealed: (i) mountain topography promotes within-species genetic differentiation of carabids among mountain regions; (ii) carabid community composition was most different between grasslands and forests, whilst deciduous coniferous plantation communities had a large degree of overlap with those from the two natural forest types; (iii) deciduous broad-leaved forests and grasslands have high spatial and temporal heterogeneity in endemic species-, family-, and order-level arthropod diversity; and (iv) landslides generate rich subterranean species-, family-, and order-level arthropod diversity. Thus, landscapes which contain multiple environmental axes increase genetic and community diversity.

Bioindicators for scarcely studied environmental axes and elements were identified during the course of these studies. Bioindicators of each taxonomic level (i.e. order-level of the kingdom Animalia, family-level of the order Coleoptera and species-level of the family Carabidae) for the environmental axes of vegetation and landslides were calculated from the data of Chapters 3 and 4 using the indicator value test (IndVal, Dufrene and Legendre 1997; Table GD-1 and 2). For the species-level analysis of the vegetation axis new indicators were identified; 8 in each of evergreen coniferous natural forests and deciduous coniferous plantations. Studies of the indicators of these two coniferous forests have been scarcely studied (but see, Yu et al. 2008).The species of the genus *Amara* (Coleoptera: Carabidae) and *Harpalus* (Coleoptera: Carabidae) were selected as indicators for grasslands (Table GD-1). These species have also previously been shown to be grassland indicators, and have flight ability as well as eat the seeds and roots of grasses and herbs (Kirk 1972; Jorgensen and Toft 1997; Klimes and Saska 2009). These indicator value test also found new order- and family-level bioindicators for the environmental axis of vegetation (Table GD-1); 6, 2, 1, 5, and 4 order(s) and 4, 2, 4, 0, and 1 family(families) were selected as indicators for grasslands, forests, deciduous broad-leaved natural forests, and deciduous coniferous plantations, respectively. Previous studies have suggested only species-level indicators, all in Lepidoptera and Coleoptera, for grasslands and some kinds of forests (e.g. Bohac 1999; Inoue 2003; Tothmeresz et al. 2014), and higher taxonomic levels have not been studied.

New indicators were also found in the analyses of the landslide axis: 7 and 1 order(s), 4 and 1 family(families), and 21 and 13 species were selected as indicators for landslides and undisturbed areas, respectively. Although several studies have reported the species lists of taxa collected from Superficial subterranean habitat (SSH) (e.g. Ruzicka 2000; Culver and Pipan 2008; Culver and Pipan 2009; Růžička et al. 2013), this is the first study to detect statistically significant bioindicators for landslides and will help promote efficient environmental evaluation. The detection of some of the order- and family-level bioindicators can be explained after consideration of their ecology. The order Collembola inhabits the soil O horizon (i.e. litter cover) of the forest floor, and the family Elateridae inhabits open habitat. Therefore, the detection of these groups as bioindicators

in forest types and grasslands, respectively, is not surprising. However, validation of- these bioindicators by proper quantitative and statistical procedures are still required. Finally, the genus *Synuchus* (Coleoptera: Carabidae) was identified as an indicator for both vegetation type and landslides (Table GD-1, 2). All three species of the genus collected in Chapter 4 were indicators for undisturbed areas (Table GD-2). In contrast, each species of the genus collected in Chapter 2 was an indicator species for grassland, forest types, deciduous broad-leaved forest, or deciduous coniferous plantations (Table GD-1).

There were some vegetation and landslide generalists at the order- and family-level, but not at the species-level (Fig. GD-1, 2). These results suggest that the reaction to environmental axes varies depending on the taxonomic level, and preferences for a specific environmental element are strongest at the species-level. Thus, in the case of the environmental evaluation, the species-level analysis is an easy and efficient method to find bioindicators, whereas the community-wide approach, which requires more effort, is necessary to find bioindicators at high taxonomic levels. For the environmental axis of vegetation, the numbers of indicator species were highest in grasslands (30% of the whole number of species; Fig. GD-1), and for the landslide axis the number of indicator species across all taxonomic levels was highest in landslide areas (50%, 44%, 61% of the whole number of orders, families, and species, respectively; Fig. GD-2). Thus, these environmental elements, which are very limited in area in a mountain landscape, help to maintain regional arthropod diversity. The effect of spatially limited environmental elements on arthropod diversity was high at the species-level in the vegetation axis, and at the family- and order-levels in the landslide axis, thus the taxonomic levels of bioindicators differ between environmental axes.

In Chapter 1, the genetic differentiation of carabid species populations may have been promoted by a mixed landscape of mountain peaks and valleys. In Chapters 2 and 3, high arthropod diversity is maintained by a mixture of multiple vegetation types. In Chapter 4, the effect of a mixture of landslide and undisturbed areas increased the diversity of arthropods. These findings support previous studies which have reported that naturally disturbed areas, such as following fires and avalanches, increase regional plant diversity (Bebi et al. 2009; Perry et al. 2011), and also that heterogeneity in elevation and geography maintain high levels of plant diversity (Dufour et al. 2006) and may even promote speciation, e.g. grasshopper (Knowles 2000). This thesis examined arthropod biodiversity formation, focusing on important and new environmental axes using the community-wide approach. The composition of multiple environmental elements in a landscape was revealed to have an important role in creating and maintaining arthropod diversity, new environmental axis evaluation methods that can detect habitat preferences across multiple taxonomic levels were established.

Tables of general discussion

Table GD-1 The list of bio-indicators at each taxonomic level (i.e. order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae) calculated by the indicator value test (IndVal, Dufrene and Legendre 1997) for the environmental elements of the vegetation environmental axis. The significance levels of the bio-indicator values are shown (*** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 9999 permutations).

	Vegetation environmental axis					
	Grassland	Forest	Evergreen coniferous natural forest	Deciduous broad-leaved natural forest	Deciduous coniferous plantation	No bio-indicators (generalists)
Order-level in Animalia	Lepidoptera ** Haplotaxida Orthoptera Julida	Collembola ** Mesogastropoda	Psocodea	Neuroptera Scolopendromorpha Oniscomorpha Colobognatha Stylommatophora	Mecoptera Nematophora Dermaptera Rodentia	Lithobiomorpha Tubificida Polydesmida Hemiptera Araneae Coleoptera Opiliones Geophilomorpha Acari Diptera Hymenoptera Isopoda
Family-level in the order Coleoptera	Elateridae ** Scarabaeidae	Cerambycidae Silphidae		Erotylidae Lucanidae	Leiodidae	Carabidae Curculionoidea

	Tenebrionidae			Cantharidae		Staphylinidae
	Cicindelinae			Lycidae		Chrysomelidae
Species-level in the family Carabidae	*Pterostichus samurai*	*Carabus (Leptocarabus) procerulus* *	*Pterostichus polygenus*	*Synuchus melantho*	*Synuchus arcuaticollis* *	
	Pterostichus planicollis	*Synuchus cycloderus*		*Nebria sadona*	*Synuchus agonus*	
	Hemicarabus tuberculosus	*Trigonognatha aurescens*		*Trephionus kinoshitai*	*Pterostichus subovatus*	
	Amara obscuripes	*Pterostichus microcephalus*		*Damaster blaptoides*	*Synuchus takeuchii*	
	Pterostichus haptoderoides japanensis	*Pterostichus takaosanus*		*Notiophilus impressifrons*	*Amara congrua*	
	Harpalus bungii			*Pterostichus sp.*	*Parabroscus crassipalpis*	
	Amara chalcites			*Pristosia aeneola*	*Dromius prolixus*	
	Amara ovata			*Pterostichus asymmetricus*	*Synuchus congruus*	
	Synuchus dulcigradus					

Table GD-2 The list of bio-indicators at each taxonomic level (i.e. order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae) calculated by the indicator value test (IndVal, Dufrene and Legendre 1997) for the environmental elements of the landslide environmental axis. The significance levels of the bio-indicator values are shown (*** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$; 9999 permutations).

	Landslide environmental axis		
	Landslide area	Undisturbed area	No bio-indicators (generalists)
Order-level in Animalia	Dermaptera ***	Mecoptera *	Diptera
	Chordeumatida *		Hymenoptera
	Grylloblattodea **		Coleoptera
	Geophilomorpha		Collembola
	Pseudoscorpionida		Lithobiomorpha
	Opiliones		Araneae
	Isopoda		Scolopendromorpha
			Julida
			Polydesmida
			Acari
			Orthoptera
Family-level in the order Coleoptera	Histeroidea *	Leiodidae *	Staphylinidae
	Ptiliidae		Carabidae
	Elateridae		Silphidae
	Lucanidae		Scarabaeidae
Species-level in the family Carabidae	*Pterostichus spiculifer* **	*Synuchus cycloderus* *	
	Colpodes kyushuensis *	*Synuchus melantho* *	
	Pterostichus okutamae	Relative of *Pterostichus asymmetricus*	
	Pterostichus sp. 1 *	*Synuchus agonus* *	
	Synuchus arcuaticollis	*Synuchus tanzawanus*	
	Trechiama kinoshitai	*Nebria sadona*	
	Pterostichus rhanis	*Pterostichus abaciformis*	
	Pterostichus katashinensis	Relative of *Trechiama leptopus*	
	Yukihikous sp. 1	*Trechiama aurescens*	
	Brachinus stenoderus	*Synuchus takeuchii*	
	Relative of *Colpodes uenoi*	*Parabroscus crassipalpis*	
	Ohmopterus esakii	*Trechiama* sp. 1	
	Pterostichus masumotoi	*Carabus (Leptocarabus) procerulus*	
	Pterostichus mitoyamanus		
	Pterostichus polygenus		
	Pterostichus subovatus		
	Synuchus atricolor		

Pterostichus sp. 2
Pterostichus sp. 3
Pterostichus tokejii
Pterostichus asymmetricus

Figures of general discussion

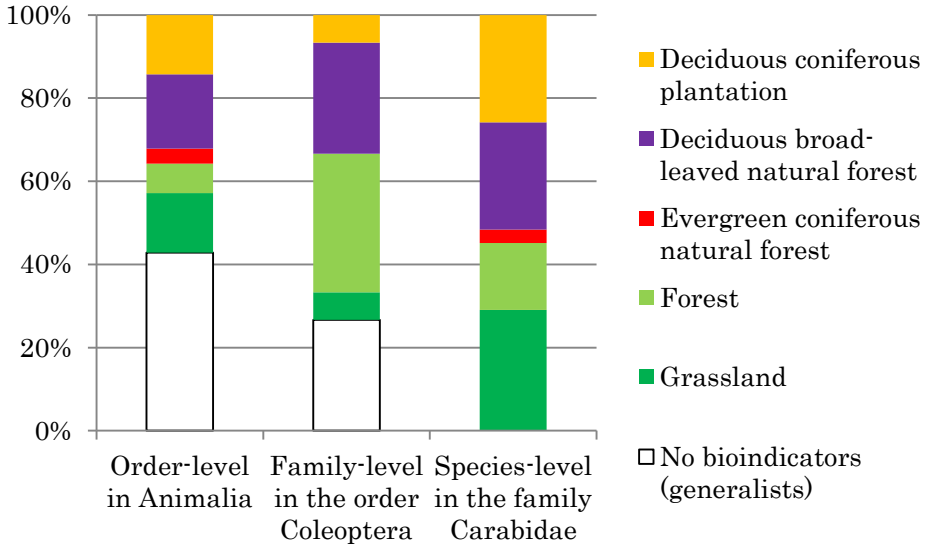

Figure GD-1 Proportions of bioindicators at each taxonomic level (i.e. order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae) calculated by the indicator value test (IndVal, Dufrene and Legendre 1997) for the environmental elements of the vegetation environmental axis.

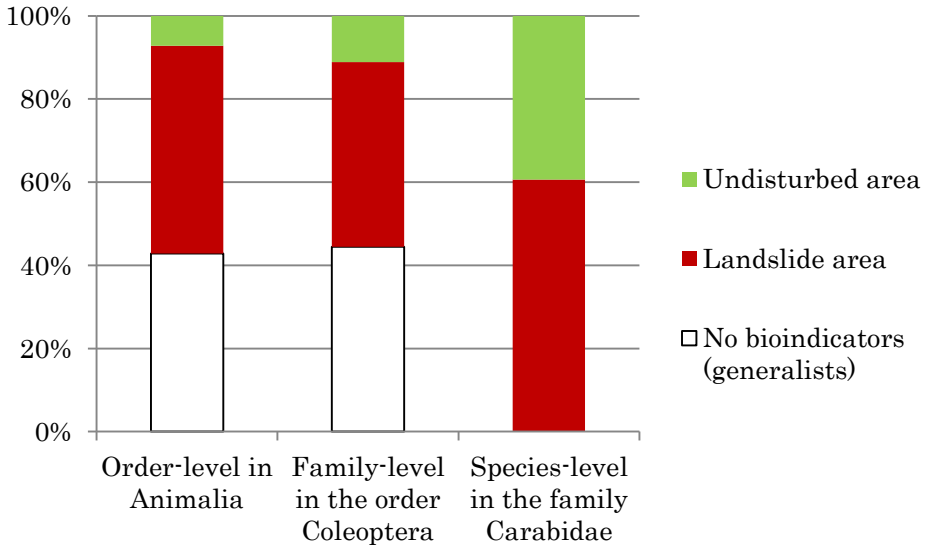

Figure GD-2 Proportions of bioindicators at each taxonomic level (i.e. order-level of Animalia, family-level of the order Coleoptera, and species-level of the family Carabidae) calculated by the indicator value test (IndVal, Dufrene and Legendre 1997) for the environmental elements of the landslide environmental axis**.**

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